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AN ESSAY ON EVOLUTION AND MODERN GENETICS. By H. GRAHAM
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"I desire no greater certainty in reasoning, than that by which chance is excluded from the present disposition of the natural world. Universal experience is against it".

Paley 1802.

The researches of the modern geneticists along Neo-Mendelian lines have produced such a vast array of imposing results that it is not surprising that the majority of scientists—not only biologists—assume that this particulate type of inheritance constitutes the whole basis of heredity. In the following essay I have tried to put the case that there may be another type of inheritance, more primitive and of more fundamental importance to the problem of evolution. I have avoided as far as possible all genetical technicalities in the hope that thereby it may be intelligible to scientists generally.

In the decade after the First World War the conflict in evolutionary thought was between those who believed in a possible Mendelian explanation and those who accepted the inheritance of acquired characters as an established fact and called themselves Lamarckians. This dualism has now disappeared. For one thing a belief in the inherited effects of use and disuse is held almost in derision by the majority of modern biologists and largely on the grounds that all attempts to prove experimentally the existence of such inheritance have been futile (Carter 1951, p. 4). The fact that such experiments as have been attempted, because of their construction have been doomed *ab initio* to failure, appears to have been largely overlooked (Cannon 1954, p. 232)*. On the other hand, for the last thirty years generations of biological students have been brought up on the firm idea that the characters of an organism are inherited according to a Mendelian gene-complex mechanism. Thus, Waddington broadcast the positive statement that "... the characters which an animal or plant inherits are controlled by a series of separate and discrete hereditary units commonly known as genes ..." (Waddington, 1952 *a* p. 759), that is, *all* the characters of an organism: not only the structural features of the adult but those of the embryo and not only the morphological characters but the physiological as well. The habits of the organism, that is the way in which the various parts of the body are used, must be considered as inherited through a gene complex just as much as the structures themselves.

Now this almost complete swing over to a belief in Mendelism as a panacea for all evolutionary troubles is not surprising from one point of view but from another aspect it is indeed remarkable. It is not surprising in view of the brilliant Mendelian research which has been carried out for the last fifty years. Thus there are very few nowadays who refuse to accept this modern work which proves objectively not only the existence of genes on the chromosomes but their arrangement, transformations and gymnastics within those chromosomes. On the other hand, it is surprising

* Since writing the article referred to I have unexpectedly come across a statement by MacBride where he clearly sees the difficulty of establishing experimentally the proof of the inheritance of acquired characters. It occurs in his Presidential Address to Section D of the British Association at their meeting at Newcastle-on-Tyne in 1916, that is, some years before he became so interested in 'Lamarckian' experiments.

in that it is only just now becoming apparent that the Mendelian hypothesis, by its very nature, is capable of explaining any results. Thus Waddington has even suggested a Mendelian explanation of the inheritance of acquired characters (Waddington, 1942, p. 563, 1953, p. 137). As Dobell (1924, p. 189) said thirty years ago referring to the chromosome theory of inheritance, "one cannot but admire the industry and ingenuity of its architects and artificers".

Of course, the attitude of modern Mendelians to their hypothesis, the emphasis placed on various parts and so on, has changed considerably of recent years, but it is doubtful if anything much has been added to the original idea. The main stumbling block to the development of the Mendelian idea appeared when it was realized that the hypothesis of unit genes for unit characters was unworkable. The Neo-Mendelians however, have dealt with this difficulty. Thus in cases where it is not possible to identify experimentally "separate Mendelian genes, the situation can be understood *if we suppose* (my italics) that we are dealing with many genes each with too small an effect to be distinctly recognized" (Waddington, 1952 *a*, p. 759)—this appears to have produced a marked change and advance in Neo-Mendelian thought. But it is nothing new. The idea was established in the early years of the century when it was shown experimentally that genes can have effects sometimes big and sometimes small and further that the appearance of one character may be due to more than one gene. This is all that is necessary and the surprising thing is that in view of this omnipotence of the Mendelian hypothesis, such a distinguished geneticist as Waddington should ask "Is there any limitation on the kind of evolutionary change which our theories would account for?" (loc. cit.). Surely the answer is no. As Carter says (1951, p. 266), "It is easy to imagine mutations that will act in any way we choose". The Mendelian hypothesis allows for all eventualities so that while it must be accepted that the appearance of any character may be due to a gene complex, it is not possible to prove that such an assumption is incorrect.

However, there is a considerable difference between this point of view and the firm belief which is being instilled into students at all levels wherever biology is taught that the characters of an organism, that is *all* its characters, are without any question of doubt the product of its genes resident in its chromosomes. It has become almost an article of faith with undergraduates arriving at the university that, however ignorant they may be about other aspects of biology, they know all about the gene complex.* The idea that, after all, characters are not all alike and that therefore perhaps they are inherited according to more than one genetic system does not seem to have been put to them. And yet in a recent book dealing with animal evolution Carter (ibid. p. 94) has pointed out that the origin of *new* structures in an organism has never been shown to be due to the occurrence of Mendelian mutations. This surely has been obvious for many years, for the mutations which are the basis of all Mendelian experiments are changes which occur in *existing* structures. And yet it is the appearance of new characters in organisms which marks the boundaries of the major steps in the evolutionary scale.

The distinction between these two types of characters is obvious to any comparative anatomist and yet it is difficult to define precisely the exact difference between them. The case which Carter (ibid. p. 94) takes is that of the evolution of the horns of *Titanotheres* from slight thickenings of the upper surface of the skull. It may be argued that this is nothing but a modification of something (the upper surface of the skull) already existing and therefore represented, according to Mendelian principles, somewhere in the gene complex. A case which may illustrate this point more forcefully is the evolution of the horn of the modern rhinoceros. This horn, as is well known, is a mass of fused hairs. It may be argued therefore that the appearance of the rhinoceros horn is not a new character but simply a modification of a patch of hairs on the snout region of the ancestral type. This argument,

* Were we not told that the real reason why Bannister broke the record for the mile was because of his gene complex? (R. D. Shaw 'Manchester Guardian', 21 May 1954).

if continued, would lead, as Dr. Carter has pointed out, to a *reductio ad absurdum* for it would imply that all the pattern of, let us say, a mammal must be already present in the gene complex of whatever can be considered its earliest ancestor.

However, despite this difficulty, it is clear that there is a sharp distinction between the mutations which form the experimental basis for Mendelian analysis and those which appear at the boundaries between one evolutionary level and another. The former can be looked upon as transformations or variations of a particular pattern or theme, the latter as definite additions to that theme.

Thus at the boundary between the Cyclostomes and Gnathostomes there appeared the fins with all their potentialities for vast specialization. They arose from existing regions of the body wall. But it matters little whether or not they are regarded as new structures or modifications of old. The important thing is that they represent an addition of something new to the *organization* of the body. In the evolution of the Reptiles from the lower forms, the Amphibia, the egg became provided with the albumen which simulates the aquatic environment of the Amphibia and the shell which prevents the drying up of that albumen. It is easier to regard these definitely as something new as there does not appear to be anything corresponding to the albumen and shell in the amphibian egg. As a third example, at the evolution of the Mammalia from the Reptilia there appeared that vital homeostatic principle of 'warm bloodedness' and to suggest that this is not a new character is surely merely a play on words.

The few examples I have quoted I have chosen from the vertebrate series because they will be most familiar to scientists generally, but similar cases, even more striking, can be found in the Arthropod stem, and, in fact, throughout the animal kingdom.

I have said that these cases where new structures appear occur at the major steps in evolution: but one can go further than that. If one passes up the classificatory tree, starting with the animal kingdom, passing through phyla, classes, orders, and so on up to species and finally individuals, then it is clear that at the bottom of the tree all the changes are associated with the appearance of new characters while at the top it becomes progressively obvious that the changes are more likely to be a result of modifications of old characters rather than in the appearance of new ones until finally the distinction between individuals is definitely a matter of variation of old characters. It must be remembered of course that the distinction between various levels of the phylogenetic tree and more particularly the distinction between family, genus and species is purely a subjective idea. But nevertheless whatever views are taken as to what distinguishes a family from a genus, it is clear that at the top of the tree the differences are of the type that one expects to find in Mendelian experiments, while at the bottom they are all dependent on the appearance of new structures or habits and so not of the Mendelian type at all.

Is it not reasonable in view of this analysis to consider the possibility that while the type of evolution at the top of the tree, the ultimate speciation of forms, appears most probably to be due to a Mendelian mechanism, that taking place lower down at the major dichotomies may be due to some entirely different mechanism?

This idea has been met, albeit accidentally, in the hypothesis of aristogenesis (Osborn 1934) but this, like the whole of Mendelism, appears to be a particulate type of inheritance. It postulates the existence of aristogenes which are responsible for the appearance of any *new* characters. Now, whatever the word 'aristogene' may mean, it must be admitted that it is a very unfortunate word for the only evidence for the existence of aristogenes is that the characters controlled by them have never been shown to obey Mendel's law. In other words, an aristogene has nothing to do with a gene and surely nowadays it can be taken that 'gene' means simply that entity concerned with inheritance according to Mendelian law.* But

* Muller (1947) in his Pilgrim Trust Lecture on 'The Gene' uses the word with this meaning. He quotes other cases of compound words such as 'plasmagene' which are definitely different from 'chromosomal genes' but, at least in these cases, whatever they represent, there is evidence that they are particulate. In the case of 'aristogene' there is no such evidence any more than there was any real evidence for Darwin's 'pangenes' as particulate structures.

the coining of the word illustrated forcibly the attitude of so many biologists to genetics today. If facts are found which do not fit into the Mendelian hypothesis, then some means must be found, some variation on the Mendelian theme must be composed, which will fit the facts into the Mendelian fabric, and as both Waddington and Carter have pointed out, this is a very easy task. The idea that, after all, there may be a type of inheritance alongside Mendelism, but having no relation to genes or even to chromosomes, some type of inheritance not particulate but organismal, is rarely thought of nowadays.

And yet there is much evidence, brilliant experimental evidence, in favour of such an idea. The whole of the results of modern experimental embryology surely point in that direction. All the work of Spemann and his school on the amphibian gastrula illustrates the action of the organism (the gastrula) as a whole. Thus in the experiment where the early embryo of a newt is caused by constriction to develop into two perfect embryos, these embryos each develop into an organism acting as a whole—not as a half—and produce embryos which are of normal proportions but small. There is the even more striking experiment in which two early embryos are each cut into two pieces by cuts to one side of the median plane, but one on the right side and one on the left. This produces two small pieces and two large pieces. These pairs can then be stuck together when they develop as composite organisms, one smaller than normal and the other larger, but in both cases absolutely normal in their proportions. I mention this case especially because it illustrates a case discussed by Waddington (1952 *b*, p. 805, also 1953). He refers to the fact that if an eyeball is produced experimentally in an animal which is larger than normal, then the lens induced by that eyeball will be correspondingly larger. This is exactly what happens in the larger composite embryo I have just described. Waddington looks upon this as control by some Mendelian mechanism and it is impossible to show that he is wrong: but is it not more likely that the organism acting as a whole is controlling the relative size of its different parts by some mechanism other than that of the gene complex?

There is another type of experiment which illustrates this point even more strongly. I refer to those experiments where patches of cells of amphibian embryos are grafted into strange positions in the embryos of different species or even of different genera. Thus it is possible to take a patch of cells that would normally give rise to, let us say, ventral body wall and graft it into the embryo of another species in such a position that it is caused to develop into the gills of the developing tadpole. Now these gills have patterns characteristic of each species and in the experiments I have just described, the grafted patch of cells develops the pattern characteristic of the species from which it came and not of the species into which it is put. This may be capable of a Mendelian explanation but, to my mind, it is far more profitable to take it as evidence of a totally different type of character in the organism. The organism as a whole controls the important functional character, namely that the embryo must have gills on hatching and so forcibly causes a patch of strange cells not normally associated with gills to develop nevertheless into a gill. Now the embryos used in the experiment 'in their former (phylogenetic) experience' cannot have 'encountered anything of the kind before' (Berg, 1926, p. 42). It is difficult to see therefore how through the agency of Natural Selection (which is essential to the Neo-Mendelian view (Waddington, 1952 *b*, p. 805)) they can have collected the necessary gene complex to deal with the situation. But the trivial character, the pattern of the gill, which probably has no effect on its efficiency as such, and which undoubtedly is controlled by the gene complex, this develops on its own, independent of organismal control.

There does not appear to be any *a priori* reason why this should not be so. The idea of the organism as a whole controlling the appearance of structures is no more mysterious than the idea of the genes within the cells influencing the appearance of characters: in fact, the reverse is the case. The whole of experimental embryology and of the work done by Child and his school on axial gradients demonstrates so

clearly the control of the development of an organism by that organism itself, and even throws light on the way in which that control is effected, and yet we have little positive evidence as to how a gene complex produces its result.

Now to the Neo-Mendelian and even also to the simple Darwinian this possible difference between the means of inheritance of the major functional characters and of the trivialities of pattern does not appear necessary. Both demand merely "the wholesale development of random variation as the raw material on which natural selection may act" (Wood Jones, 1953, p. 155). That is all they require and this is the view which was put forward very forcefully over the air by Waddington. In his broadcast he said "the present theory bases itself essentially on the idea that new hereditary changes occur spontaneously and at random: that is to say . . . they . . . are not guided so as to fit into the environment but can alter the animal in any and every way" (1952 *b*, p. 805). If they happen to be advantageous then they are established by means of Natural Selection. In other words, given time, "then eventually anything at all will turn up" (*loc. cit.*). Thus if the lens of the eye of a newt is removed, the animal has the power of regenerating that lens. It does so not by the process of the eyecup inducing the overlying skin to produce a lens as happens in normal embryology but by something quite different, by a special growth of the margin of the dorsal iris (Reyer, 1954, p. 1). Now this ability is a character and hence must be represented in the gene complex but what is more important, according to Waddington, must have been established as a successful character by means of Natural Selection. This must be an example of what he means when he says that anything at all will turn up. Now how often has Natural Selection had the chance of acting in such a case? How often does a newt have its lens extracted so that Natural Selection can act? It is not surprising that Waddington admits that even to him 'modern evolutionary theory is too flexible' (*loc. cit.*).

What Waddington is referring to as 'the present theory' is the Neo-Mendelian hypothesis and this involves the conception of 'genes' and of 'characters' as things which are clearly definable. Now the existence of genes as particles arranged in a linear series along the chromosomes has been proved by experiment as firmly as anything can be 'proved' in biology. But the theory demands that there are characters corresponding to these genes, not necessarily one gene for one character—that is the old-fashioned view—but possibly many genes producing a single character. Now it is here that the difficulty arises—a difficulty pointed out more than 30 years ago by Johannsen (1923, p. 136), the inventor of the term 'gene'. For while the gene is *ex hypothesi* a single entity—a particle—it is extremely difficult to discover any character of an organism which, on analysis, turns out to be simple. In fact Johannsen states 'there are no unit characters at all!' and then adds 'Undoubtedly all scientific geneticists now are or ought to be in accord as to this matter'. In this he seems to have been somewhat over-sanguine.

The fashionable view is to regard the development of any organ such as, for example, the eye as a series of chemical reactions taking place in a particular order so that any particular reaction is always dependent on all the preceding reactions having taken place normally. In such a sequence of events it is clear that, if in one of the *early* reactions a necessary constituent is absent, this results in the whole series being suppressed and hence, in the case we are considering, the non-appearance of the eye. It is simple to imagine a mutation in a particular gene acting in such a way as to be responsible for the absence of that particular constituent. But what the majority of students do not realize is that the appearance of the original gene in the course of evolution would not lead to the establishment of the rest of the series of reactions necessary for the appearance of the eye.

An analogy may emphasize this critical point. The modern motor car has evolved by virtue of the powers behind the scenes, the manufacturers, who in competition with each other produce better and better types. If they produce an inefficient type then this does not sell and so disappears from the market. So we have a case analogous to the evolution of more and more complicated organisms

with natural selection weeding out the unfit types. The actual making of a car—its embryology—consists of a series of processes taking place one after the other and all being dependent on the earlier processes having taken place normally so that again we have something closely akin to the embryonic development of an organism. Now in the modern world with the progressive increase in bureaucratic control all the stages in the manufacture of a car become dependent on more and more rules and regulations having been complied with. Not only is a supply of the necessary material essential at each stage but there are permits to be obtained, government regulations to be complied with or trade union demands to be satisfied. Now the absence of any permit or the non-compliance with any regulation will interfere at once with the manufacture of the car. Thus the absence of a permit giving permission to start the manufacture of the car puts a stop at once to the whole embryology of the car. But it was not the establishment of the permit system that led to the evolution of the car. This took place quite independently of bureaucratic control. The permits came later and whether or not the permit system was established, the evolution of the car would still have taken place with just the same efficiency and success. Is it not possible that the eye evolved in just such a manner quite independent of any gene for the presence or absence of an eye? Is it, in fact, not more probable that it evolved in spite of its gene complex and not by virtue of it?

To return to this general complexity in the nature of the characters of an organism, let us consider any muscle in the body. Take for example the biceps muscle which raises the forearm. Now this may be a simple muscle, but its action is never simple for it never acts alone. Its contraction involves a whole series of other muscles. More than that, without the appropriate and nicely balanced action of these ancillary muscles, the biceps cannot function properly, and therefore could not evolve properly. As Wood Jones points out (Wood Jones and Porteus, 1929, p. 195) “. . . with the rarest exceptions, muscles taking part in voluntary action do not act as individual entities but as groups”. And he could have gone further than that, for the complex of muscles related to any one such as the biceps varies with the posture of the body. Thus, sitting writing at my desk and raising my pen, a certain number of muscles must co-operate to allow the biceps to function. But if I lean over from a standing position to pick up something, then the complex of muscles involved is so great as to involve almost the whole muscle system. But how is all this to be represented in the gene complex? The presence of a biceps muscle, being a character, demands that it shall be represented by a definite gene or genes. Now is there one gene for the biceps muscle complex, and if so, what are its limits, or are there separate genes for each individual muscle?

However, whatever the answer to this may be, the theory further demands that it is through *random* changes in the genes concerned that the evolution of the biceps muscle must have been brought about. But if at every stage the biceps muscle depends for its efficiency on the existence of a set of other muscles all appropriately placed and all of the proper strength, the random changes in the genes which produced the random changes in the biceps muscle in the course of its evolution must have involved, not random changes in those other muscles, but closely correlated changes.

It may be argued however that these correlated changes are brought about by purely mechanical stresses and strains. Thus if the biceps muscle enlarged at one mutation it would automatically put additional strain on some particular ancillary muscle which would accordingly increase in strength and thus whatever happened to the biceps muscle, there would always be a nicely balanced set of related muscles. This may involve an acceptance of the idea of the inheritance of the effects of use and disuse but this holds no terrors nowadays for the really modern Neo-Mendelian. In any case it is no real explanation. As Berg points out (1926, p. 11) we do not know why added stimuli should produce increase in the size of the muscles and surely it is begging the question for Waddington (1953, p. 137) to say “. . . one of the main characteristics of animal development is that it tends to be canalised or buffered, so that the optimum end result is produced”.

However, instead of considering a muscle and its related complex let us think of the armature of an arthropod. Throughout this group the exoskeleton, the outer covering of the jointed limbs, is armed with processes, spine-like setae and hair-like setules, and it is on the basis of most elaborate arrangements of such setal armature that the important organs such as feeding mechanisms and so on are constituted. I shall deal with such cases in some detail later. The point I wish to emphasise here is that all these exoskeletal structures are essentially dead—at least on their outer surface which expresses their form.* Hence no amount of use of a spine, a seta or a setule can possibly lead to its enlargement. Hence if one patch of setae which constitutes the central armature of, for example, a feeding mechanism enlarges, then there is no possibility of the other ancillary setae in other parts of the feeding mechanism enlarging correspondingly as a *purely mechanical effect*. And yet in the arthropod feeding mechanism there is precisely that perfectly balanced co-operation between the various parts just as there is in any muscular system in the vertebrate body.

As a third example illustrating the composite nature of structures which may appear quite simple let us consider the case of the egg hatching nodule which occurs on the beaks of birds as a means of escape from within the egg shell. This has been dealt with fully by Wood Jones (1954) and, I think, is even more striking than the cases I have mentioned. This nodule appears so very simple. It is of course, essential to the life of the bird but is quite useless unless it is used in the appropriate manner. It involves therefore (1) the simple structure itself, (2) the muscles necessary to move it in the appropriate manner, and (3) the instinctive knowledge of how to use it, and all these closely correlated characters we are asked to believe arose through random changes in the genes!

The difficulty of explaining this type of evolution has been seen by Waddington (1952 *b*, p. 805), and in discussing this point he has taken as his example, like Paley before him, the human eye. He points out how it consists of numerous relatively simple parts, all inter-related in their structure and functioning so as to produce one single organ. Random mutation, he says, could not lead to the evolution of the whole coordinated structure, for the chances of all the mutations occurring in the same direction at the appropriate time are so remote as to be negligible. He postulates, therefore, in the eye, a regulatory mechanism whereby, if one part changes in one direction, then all the other parts change adaptively and therefore he states there is no reason “why a chance mutation should not affect the whole organ in a *harmonious way*” (my italics). There is no doubt that this harmonious control *does* act in the embryology of the eye—experimental embryology has proved that—and Waddington who is a distinguished embryologist is merely suggesting that this same control could act during the evolution of the eye.

But what is this ability of the parts of an organ to react in such a way as always to produce a perfectly efficient functioning organ? Is it not a character in itself and, moreover, one of paramount importance? And as such must it not be represented in the gene complex? The Neo-Mendelians cannot escape this deduction: in fact, Waddington in a later publication (1953, p. 136) admits this.

But then, if it is represented by a gene, it means that, again *ex hypothesi*, it must have evolved by hereditary changes that occurred ‘spontaneously and at random’ (Waddington 1952 *b*, p. 805) and it is indeed difficult to see how on Mendelian grounds this could have come about. There seem to be two possibilities—either that at every stage in the evolution of the eye an appropriate gene appeared whose function was to see that with the next mutation of any part of the eye, the remainder of the eye

* My colleague, Professor Dennell, has pointed out to me that Wigglesworth and others have shown that shortly after a moult, while the external surface of the body of an arthropod is still soft, there may be a small amount of growth of spines or even the appearance of new spines under the stress of new conditions. This does not however invalidate what I have said above, for during this short period after ecdysis the animal is almost out of action—it is only *after* the exoskeleton has become hard and rigid that the animal develops again its full activity.

responded 'harmoniously'. Either this, or that at the very beginning of the vertebrate eye series, a gene appeared that is still present in the human complex and which has carried out the same function. The first possibility is ruled out on grounds of probability—it is "something which one could not expect to occur under the influence of chance alone" (Waddington, loc. cit.). But the second possibility is even worse because it means that the plan of the human eye must have been present somehow in the gene complex of the animal that first evolved the primordial eye for an ever present gene cannot have controlled the development of the eye complex 'harmoniously' unless the ultimate end was established at the beginning. And this is the *reductio ad absurdum* which I mentioned when discussing aristogenes, for it implies that all the genes connected with the eye must have been present in the earliest chordate from which the vertebrates evolved. Do the Neo-Mendelians really believe this?

That this harmonious control is present in all organisms seems to be accepted by the comparative anatomist, the embryologist and the Mendelian alike. But is there any substantial difference between it and the 'entelechy' which Driesch postulated long ago, also on the grounds of experimental embryology, and got laughed at for his pains (see MacBride, 1916)? His entelechy was a "rudimentary psychoid which knows and wills what it wants to produce" and was somehow resident in the embryo. The embryo 'knew' how to develop itself. Is not Waddington applying the same idea to the evolution of an organism? The organism 'knows' how to evolve. This seems to be agreed on all sides but the real point at issue is as to whether this coordinated evolution is due to the changes that occur spontaneously and at random, for the Neo-Mendelians cannot escape this, or whether it is directed.

Wood Jones (1953) has recently put forward a strong case for directiveness in evolution. His examples are mostly taken from his very wide experience of the vertebrates. I wish now to add what appear to me similar cases from the group with which I am most familiar—the Crustacea.

First, however, there is a general case which Wood Jones might have mentioned as a vertebrate example. It is the fact that in the blood systems of the vertebrates valves always appear at appropriate places along the course of the blood vessels and so constructed and orientated as to ensure the passage of blood in one direction. This is not confined to the vertebrates but is found throughout the invertebrates, for example among the annelid worms. Now from the Annelida evolved the Arthropoda and hence the Crustacea. During the course of this evolutionary step the blood vessels swelled to such an extent as to occupy the whole body cavity and, apart from the heart which represents the dorsal longitudinal blood vessel of the worm, blood vessels as such disappeared and with them of course their valves. In the barnacles, even the heart disappeared, but despite this there is in this group, a perfect circulation. This has been made possible first by the development of a parenchymatous tissue filling up most of the body cavity but leaving narrow channels which function as blood vessels. They have nothing to do with the blood vessels of Annelids. They are certainly new structures. Then a new pump has appeared which by its contraction can force the blood into these vessels. But the point I wish to make is that once again valves appear in these vessels and at just those places which ensure that the blood circulates in one way round the body. Without these valves this newly developed canalicular blood system would be useless for the blood would merely surge backwards and forwards in the vessels under the influence of the blood pump. Valves were necessary and so they appeared. This is what according to the Neo-Mendelians and according to Darwin we are asked to believe is the result of random variation!

The second case I wish to deal with is that of the filtratory feeding mechanisms of the Crustacea. These are valuable as examples in our present discussion as they can be analysed very simply into their constituent parts. Furthermore they are very clearly defined—there is not the same difficulty in defining their limits as there is in an organ such as an eye or a muscle.

A filter feeding mechanism is a mechanism whereby the animal possessing it filters water from its immediate surroundings and collects the residue as food. In the Crustacea it always consists of interrelated limbs or parts of limbs arranged in special relationship to the mouth. It is made up of a few definite parts. First, of course, there must be a filter. This consists of a plate of parallel setae whose edges are armed with setules which always face the direction from which the water to be filtered comes to the filter plate. Secondly, there must be some form of apparatus—a pump—which causes the water to pass through the filter and may be a vibratory paddle-like plate on a limb behind the filter. Thirdly there must be an apparatus by which the filter plate is cleaned from its filtered residue. Clearly this is essential for otherwise as the filter plate carried out its function its meshes would become clogged with residue and proportionately as this happened, the filter plate would become less efficient. Finally since the residue serves as food for the animal there must be a transport apparatus to pass the collected food into the mouth.

These four constituent parts can be found in every filter feeding crustacean and it is clear that any alteration occurring in any one of these parts during their evolution must have involved all the others, for if they did not alter in an appropriate manner then the whole coordinated mechanism would become less efficient and would tend to be wiped out by selection. Thus suppose that by some mutation the filter develops a finer mesh, that is, it becomes more efficient as a filter. Then clearly, since the mesh of a filter determines its resistance to the passage of water through it, the pump must also mutate so as to become more powerful—thus the vibratory plate would become larger. But then it is of little use the filter collecting more residue unless the rate at which it is scraped off the filter is also increased. Thus the scraper must develop more accurately to fit the filter plate that it cleans. Finally if more food is being collected then the transport apparatus must increase in its power accordingly.

Now the arguments that Waddington used against the idea of the individual parts of the eye mutating separately and yet leading to a coordinated structure apply equally here. There must be a controlling influence—a guiding force—but once again this is a character and hence on Mendelian grounds must be represented in the gene complex. We are however up against a further difficulty. In the case of the human eye we are dealing with a structure that is generally speaking typical of all the vertebrates. "Throughout the vertebrate series the basic eye pattern persists with remarkable consistency" (Romer, 1950, p. 509). It is therefore just possible to imagine a gene controlling harmoniously the variations of eye pattern throughout the existing modern vertebrates. But this cannot apply to the filter feeding mechanism of the Crustacea for here we are not dealing with one basic mechanism showing slight modification throughout the group but with a whole series of such mechanisms all differing markedly from one another but at the same time working on exactly the same principles. They have evolved quite independently of each other and in some cases we know how they have evolved for the steps by which the most complicated have evolved from the simpler are represented by a series of mechanisms in existing crustacean forms. There are at least six different lines along which the Crustacean filter mechanism evolved. In each case it can be divided into the four constituent parts and no more, but what forms one part in one form may be totally different in another. Thus the filter in a Mysid shrimp is part of the second limb behind the mouth, in the Fairy Shrimp it is constituted by the eleven trunk limbs while in the water flea it occurs on the fourth and fifth limbs behind the mouth. The same diversity occurs among the other constituents.

Perhaps the most remarkable case recorded (Cannon, 1933) is that of two distantly related Ostracods—so distantly related as to be placed in different sub-orders. Both possess a superb filter feeding mechanism, certainly the most perfect I have ever seen. To anyone except an authority on this particular group the mechanisms would be taken as identical. The actual filters for example resemble each other so closely that any zoologist might be excused for deducing that they were homologous

structures. In fact the four constituents of the mechanism are on different limbs in the two forms. Thus the filter of one (*Asterope*) is borne on the first limb behind the mouth (maxillule) while in the other (*Cytherella*) it is on the limb at the level of the mouth (mandible). But this is not merely a case of shifting the mechanism one segment down the body—what Lankester called translocation—for while in *Asterope* the mandible only transports the collected food into the mouth, in *Cytherella* it carries the filter plate as well. It is not a case of the function of a particular limb in one form merely being shifted *in toto* to an adjacent segment in another. It is a sort of patchwork redistribution of functions to the various parts of the limbs concerned.

Thus in all these filter feeding mechanisms there is amazing structural diversity and yet the principle on which the mechanism works is the same throughout. Now on the Neo-Mendelian Hypothesis we have to believe that along each of these separate lines of evolution a guiding gene appeared to control the mutations of the separate parts of the filter mechanism, not merely harmoniously, but always towards a mechanism based on the same principles. But, and this is the crucial point, the Mendelians insist that these separate genes along these separate lines appeared by chance! Is this any "more satisfactory than appealing to a miraculous succession of miracles" (Whitman, 1904)? Let the Mendelians have their gene, for its presence can never be disproved experimentally, but let it not arise by chance.

This, as I see it, represents the central point in modern evolutionary argument. What is at issue is not whether the Mendelian gene complex mechanism has any reality. It is as to whether the changes which are necessary for evolution, whether they be due to changes in the gene complex or not, are due to chance alone. Paley defined chance as "the operation of causes without design". That is the point at issue—are the changes directed towards a design? Wood Jones says they are and so do I—but in fact we are both in different fields merely trying to produce more evidence from comparative functional anatomy for a point of view which has been put forward many times before. Berg (1926), in his "Evolution determined by law", gives a good historical account of the matter and from this it is clear that it is to Lamarck that we must first attribute the idea in any substantial form.*

Now the views of Lamarck are very much misrepresented in modern biology. What is taken to represent Lamarckism, namely a belief in the inheritance of acquired characters as an evolutionary process, is in fact only one of his four laws of evolution. It is difficult to know exactly how this came about but it looks suspiciously as though Darwin was responsible for the mistake. He did not like Lamarck's book—he referred to it in 1844 as an "absurd though clever work" and the views expressed therein as 'Lamarck nonsense' and 'veritable rubbish' (Darwin, 1887, 2, pp. 23, 29, 39). Later, in the year of publication of the 'Origin', 1859, he added a postscript to a letter to Lyell in which he said that he did not get 'a fact or idea' from Lamarck's 'extremely poor' work (ibid. 2, p. 215). But then four years later still he was even more definite and scathing in his criticism for he referred to Lamarck's work, again in a letter to Lyell, as one which he considered 'after two deliberate readings, as a wretched book, and one from which (I well remember my surprise) I gained nothing' (ibid. 3, p. 14). His memory however, must have played him false for there is evidence in a letter written to Huxley four years previously (Darwin & Seward, 1903, i, p. 125) that even then he must have had a very definite though erroneous idea as to what Lamarck's views entailed, for he suggests that Lamarck was guilty of plagiarising from his grandfather Erasmus. He would hardly have made such a suggestion if he had not felt confident that he comprehended Lamarck's views correctly. But that he did not in fact do so is clear from the passage that he quotes from 'Zoonomia' in support of his contention. This refers to the evolution

* My colleague, Professor Dorothy Emmet, points out to me that we must not forget Aristotle for, after all, he tried to explain the relation of the structure and parts of an organism to their function as the result of some organising principle guiding the arrangement of material towards the realisation in that individual of the specific type proper to it.

of the beaks of birds through the inherited effects of use—that is, it concerns Lamarck's fourth law alone.*

Darwin père however, was not alone in misrepresenting and so minimising Lamarck's views. His son, Francis, in editing his father's letters includes a chapter by T. H. Huxley in which the latter refers to Lamarck's "*one* (my italics) suggestion as to the cause of the gradual modification of species" (Darwin, F. 1887, 2, p. 189). It is not surprising, therefore, that those who followed fell into the error of regarding the idea of the inherited effects of use and disuse as synonymous with Lamarckism. Thus the eminent zoologist, Poulton (1909, p. 34), in the essays which he edited in connection with the jubilee of the publication of the 'Origin' clearly refers to the 'Lamarckian theory of hereditary experience' in this sense. But it is indeed even more surprising that during the twenties when MacBride was championing what he called Lamarckism, with such gusto against the Mendelians none of us stopped to enquire whether Lamarck's views were being correctly presented. And yet just about that time Dendy (1923) in the revised edition of his excellent book 'Outlines of evolutionary biology' published a concise statement of Lamarck's four laws as quoted in his "*Histoire naturelle des animaux sans vertèbres*" so we ought to have known what were in fact his views, and therefore what should really be included in the term 'Lamarckism'.

His first law is difficult to interpret exactly but it would seem to postulate that the evolution of organisms has been accompanied by an increase in size to allow for the more and more complicated structure, and few would disagree with this. His second law is the important one. It states that it is the *need* of a new organ that results in its production. His third law states simply that the development and effectiveness of organs are proportionate to the use of these organs, while his fourth law enunciates Lamarckism in its modern sense—"Everything acquired or changed during an individual's life time is preserved and transmitted to the individual's progeny".

In discussing these laws he states that he considers the third law "as one of the most powerful means used by nature for creating diversity among the races of animals" (Lamarck, 1835, p. 159) and further that it established the necessity of the second law 'and is indeed its proof' (loc. cit.). Without necessarily agreeing with his argument it is clear where he puts the emphasis. However, a few pages further on (ibid. p. 163) he is even more definite. Referring to the evolution of limbs, he states that it is not true that the limbs preceded the use as zoologists say, "but on the contrary, the need resulted in the appearance of the appropriate limb and developed it in proportion to its function". And again species "will remain unchanged only as long as their environment does not change and *force them to adapt themselves*" (my italics). That is, it is something in the organisms themselves, some organismal control, that leads to their purposive evolution—there is nothing left to chance—that is the essence of real Lamarckism.

Not only did the *use* of an organ lead to its development but the *need* for an organ led to its appearance. Lamarck definitely believed that if in a new environment a new organ would be required that organ would appear. Thus when the first reptiles started laying eggs on land, the aqueous milieu of their amphibious ancestors somehow had to be provided and so white of egg appeared. And to prevent this drying up a hard egg shell was necessary and this again necessitated the evolution

* It must be remembered that about this time, Darwin must have been giving considerable thought to 'Lamarckian' ideas for he wanted them for his Theory of Pangenesis. Thus in 1865 in a letter to Huxley, thanking him for reading through a manuscript chapter on this subject, he uses the expression 'such *facts* (my italics) as the inherited effects of use and disuse, etc.' And then, of course, in the sixth edition of the 'origin', the first impression of which was published in 1872, in the new chapter 7 which appeared for the first time, he openly accepted the inheritance of acquired characters in his explanation of the origin of the neck of the giraffe. He states that this came about through natural selection 'combined no doubt in a most important manner with the inherited effects of the increased use of parts . . .' (Darwin, C., p. 178) so that the 'absurd though clever work' was apparently not such 'veritable rubbish' after all.

of some means by which the embryo could escape from the hard shell. And then there was the precocious development of the cloacal bladder of the Amphibia to act in a double capacity as an excretory storage organ and as an embryonic lung. All these things were required and therefore according to Lamarck they appeared.

From this it is clear that the mistake made by Darwin, if indeed he was the first to fall into error, is not merely of academic interest. For an evolutionary hypothesis based on Lamarck's fourth law alone is, as most biologists would agree, patently untenable, while if it is combined with his second law or *even if it is based on his second law alone*, it is something hard to controvert.

Of recent years there have been two important attempts to put forward views closely similar to those of Lamarck. In 1926 Berg published his book on *Nomogenesis*. He accepts the idea of the inheritance of acquired characters and adds (p. 37) " . . . a useful variation arises just when it is needful ". And now, as I have already mentioned, Wood Jones has published his 'Trends of life' in which he says that the raw material of evolution "consists in structural adaptations brought about by the functional demands of the environment" (1953, p. 155). For myself, I accept all Lamarck's four laws on the evidence of comparative functional anatomy but at the same time accept as proved the existence of certain types of characters which are inherited through a Mendelian gene complex mechanism. I see no incompatibility in the two hypotheses and in the earlier part of this essay I have tried to make clear what appear to me the significant differences between the two types of characters.

I have said that I take as proved the existence of a Mendelian gene complex mechanism, but this itself, must have evolved and only those who understand the complexities of the process can appreciate the magnitude of this evolutionary step. It cannot have been present in the earliest forms of life as an analysis of the proof of its existence shows.* This proof is established in three main steps: (1) the correspondence between the behaviour of *chromosomes* and the behaviour of Mendelian characters during sexual reproduction, (2) the correspondence between the number of *chromosome* pairs and the 'linkage groups' of these same characters and, finally (3) the evidence derived from breeding experiments which show 'crossing over' which established that the particles representing the characters in the *chromosomes*—the genes—are arranged in a definite obligatory linear series along the chromosomes. Now it is obvious that in this proof, each of the three steps involves a conception of chromosomes which exist as actual structures. What happens therefore in those organisms where there are no chromosomes, and it must be remembered that it is possible that there are more different types of organisms without chromosomes than those with them? In the animal kingdom chromosomes strictly speaking appeared with the evolution of a cellular structure, that is, with the earliest Metazoa. The non-cellular forms—the Protozoa—do not possess chromosomes in the sense that the Mendelians use the word. There occur throughout the group thread-like staining bodies which are associated with the nuclei but these are mere simulacra of chromosomes. In the form showing perhaps the most similarity to chromosomes of higher forms—*Aggregata*—Dobell (1924, p. 189) in his most pungent style was able to show that, whatever these staining bodies are, they 'are not in themselves the material basis of all hereditary transmission'.

From the studies of the life histories of modern Protozoa it would appear that in the protozoan age, when these organisms formed the highest level of animal life,

* This view, however, is not accepted by Muller (1947). He maintains that the actual substance constituting the gene—the genetic material as he calls it—represents the primordial form of living material (p. 3). Protoplasm came later. This is an extreme Mendelian view, and I suppose is a final conclusion from the assumption that all characters *must* be produced by the action of genes. But even so I find it difficult to see how Muller can adopt this view in face of the fact that one of the things we know definitely about genes is that they themselves, that is the genetic material, never actually form structures that are caused to appear through their influence. The red eye of a *Drosophila* is not formed of genetic material for red eye! And yet Muller would go further than this and say that the earliest organisms of all—not merely structures in them—were formed of material which in higher organisms forms their chromosomes.

there occurred time and again the evolution of a process involving the fusion of two individuals, and these processes have come through to the present day as the various types of conjugation and so-called 'sexual' reproduction among modern Protozoa. But along one line of protozoan evolution there emerged the cellular type of body characteristic of all higher animals and with it, as might be anticipated, an accurate mechanism for the multiplication of cells that we know now as mitosis. Moreover the fusion, which at the protozoan level is between individuals, became along this line a fusion between separate specialized cells—the gametes—and this became the true sexual mechanism which has remained the same in all essentials from the anemones up to man and the mosquito. And with mitosis and sex came the chromosomes *sensu stricto* and hence genes. Now there is no reason to suppose that the type of inheritance which we know by experiment is associated with genes, does not go back to this earliest level at which the first cellular organism occurred, *but we have no right to assume that it went back any further*. Genes require chromosomes, and moreover they require the parallel bars of chromosome behaviour for their gymnastics, and therefore genes and hence Mendelian inheritance must have evolved *pari passu* with chromosomes.

If this argument is accepted it follows that in all those organismal types below the evolution of chromosomes, that is many protozoa, all bacteria, viruses and whatever preceded viruses, there can be no possibility of Mendelian genes. But since we know that these organisms show definite hereditary processes it follows that there must be an hereditary mechanism of a different and more primitive type—and what more natural or probable can there be than an organismal type—the organism acting as a whole and transmitting its characteristics directly?

In using this expression 'as a whole' this does not preclude the possibility that some particular constituent of an organism may be specially adapted for the hereditary process to the exclusion of other parts. Thus in some bacteria evidence is accumulating that the desoxyribosenucleic acid or some compound of that general type is definitely concerned with both the acquisition and the inheritance of certain characters. But this compound is simply a constituent of the general protoplasm of the bacteria. It is not isolated in any way but forms one of the many interacting chemicals which together form the complex which constitutes the protoplasm of the particular bacterium concerned so that its activity can correctly be considered as that of the organism as a whole.

This is a very important point because nowadays with the tremendous advances which are being made in bacteriology and biochemistry, it is most unfortunate that those chemists and physicists who become the leaders in these fields generally accept the idea from the geneticists that *all* the characters of an organism be it man himself or a bacterium are bound to be inherited through the gene complex mechanism. The fact that in the bacteria there is no trace of sex and even if the point of view is taken that they are nucleated, there is the further fact that the nuclei in no way resemble the nuclei of cellular organisms—these are overlooked. However, the bacteria are not at the bottom of the scale. Modern research in fact has shown that structurally they are far from simple. I am taking the view that they must have been preceded by viruses or virus-like organisms. I am aware of the view sometimes taken that viruses are intracellular and that therefore they could not have existed before cellular organisms were evolved, but the fallacy here is that these known intracellular forms are all pathogenic and that is how they are recognised. There is every reason to suppose that there must be a vast population of non-pathogenic forms just as there are in bacteria and protozoa. Now with the development of electron microscopy it appears that all viruses studied up to now can be identified as discrete bodies. But what is more remarkable is that it appears that they can sometimes occur in crystalline form (Smith 1951, p. 196). This suggests that we are approaching such minute dimensions that any structure in the virus bodies must be merely molecular constitution. The bodies can be looked upon as granules, as organisms without form or simply amorphous particles of living matter

or protoplasm. And further, since viruses differ from one another those differences must be due solely to differences in the constitution of their protoplasts.

Now we know that viruses can grow and yet, given a uniform environment, remain constant. Hence they must possess a definite hereditary mechanism. Now surely this cannot be anything else than a property of the whole organism. To assume that it results from the activities of genes is gratuitous for an organism without form (apart, of course, from its molecular form) cannot possess a set of hereditary units arranged in a particular order along structures, which being amorphous itself, it cannot possess.

As I see it therefore all these early types exhibit an organismal inheritance unobscured by the gene complex mechanism and it is this fundamental organismal control that I maintain has persisted right through to the present day alongside the Mendelian type of inheritance that evolved so much later.

I have spoken of the viruses and before them their precursors and I am taking the view that this is as far as we can go back in the history of living things with any degree of certainty. What living matter consisted of before then must be left to the speculation of the biochemists. There seems to be general agreement however, that all organisms from these lowest to the highest consists of complex systems of chemical reactions which are in equilibrium with the environment. They are of the type called by the chemist an open system in that "the organism is not separated from its environment, being connected with it by the influx and efflux, respectively, of nutrient material and waste products" (Bray & White, 1954, p. 74). In other words all organisms somehow take in material and use it for maintaining their own needs and as a result of the work done in this way of necessity produce other surplus chemicals which are of no use and are excreted. But what characterises the living organism from any other complex of chemical reactions is that the living matter—the protoplasm—which is constituted by the chemicals taking part in the living reaction always produces more and more material of the same sort, that is, all organisms grow. And in the very earliest stages, before living things had form, that is all we can say. They grow, but to say that they reproduce is misleading. It is only when there is a definite body form that it can be reproduced.

The equilibrium with the environment is surely a *sine qua non* for the very existence of an organism. An organism to be such must be definable and in the earliest amorphous forms of life long before cells or even body form were thought of, the only definition possible must have been that of chemical composition. There may have been systems of chemical reactions which were capable of growth and in which there was no constancy but these could not have given rise to organisms, for an organism, by definition, is something with certain definite characteristics and in the earliest living things, in the absence of any body form, these constant characters can only have been chemical composition. It follows therefore that ability to keep this constitution constant must have been one of the earliest characters of organisms. Any change in the influx from the environment or the efflux into it or, in fact, any change at all in the environment, must have produced a reaction within the organism to bring about an internal equilibrium again; otherwise the organism would be continually changing, would become undefinable and so would cease to be an organism. Now this power of self-adjustment has been called homeostasis by W. B. Cannon (1932, p. 24) and other names by a variety of earlier authors (see Berg, 1926, p. 13). The point I wish to emphasise is that it must have been present in the very earliest forms of life, and in fact must have been the only guiding principle of their lives.*

Now in such relatively simple systems it is easy to see that this homeostasis is nothing more than Le Chatelier's principle of the chemist. This states 'that a system in a steady state (or equilibrium) responds to changes in external conditions in such a way as to tend to counteract the effect of the external changes' (Bray and White,

* Since writing the above, our President, Dr. Seymour Sewell, F.R.S., who very kindly read through the manuscript of this essay, has referred me to his own address to the Asiatic Society of Bengal over twenty years ago in which he made the same point (Seymour Sewell, 1931, p. 355).

1954, p. 75). Now applying this to one of the earliest forms of life, if changes in the environment took place, the equilibrium of such an organism would be temporarily disturbed. Then that reaction would take place which would tend to bring about equilibrium again. Now this equilibrium would not necessarily be the same; in fact, if the change in the surroundings persisted and became pronounced it would most definitely be a new equilibrium. But since organism and environment are inseparable a new equilibrium means a new organism. In other words, as the environment changes the organism adapts itself to these changes and this is by virtue of the power within itself. Purposive constitution in fact is a fundamental property of living matter. Inheritance in such a form is a simple matter. There is no question of sexual or, strictly speaking, of asexual reproduction. The amorphous organism simply grows and if its environment changes it modifies itself accordingly by manufacturing the appropriate protoplasm to suit the new conditions.

This I consider is relatively easy to envisage and I cannot see any way out of these conclusions regarding the earliest stages of structureless life. The organised systems of chemical reactions which had the power of growing—the protoplasm—*must* have obeyed Le Chatelier's principle or if, because of the nature of the disturbances around them, they could not, then they would cease to exist—and this would simply be extinction by natural selection. But one thing that modern studies of living protoplasm have demonstrated conclusively is that chemical composition is not enough—a definite structural arrangement of the molecules in the living complex is essential and is always evident. And this applies not only to the surface of the protoplasm but throughout its substance. In other words a definite architecture is essential to the proper functioning of protoplasm. If this is upset the properties of the complex must be disturbed. Clearly then Le Chatelier's principle will apply here as well so that, not only will a definite *chemical* composition tend to be maintained, but a definite *structure*. Now when the first organisms with body form evolved, they must have originated from these primitive amorphous protoplasms, and they must have been of the same constitution, but simply organised into definite and characteristic entities which we call individuals. Now these individuals would have the same power as the primordial living material from which they evolved of being able to adjust themselves both chemically and structurally to a changing environment. In fact since, according to my hypothesis, the reactions of the earliest living matter can only have been changes in response to a changing environment to maintain equilibrium with that environment it follows that the first evolution of individuals with definite body form from formless granules of protoplasm must have represented simply one of those changes. If this is accepted then there is no reason why such bodily changes should not continue to evolve and for the same reasons. This is an assumption but there is plenty of evidence to support it. We know that particular types of protoplasm are capable of building up particular types of structure. One has only to watch a complicated protozoan with half a dozen different types of cilia dividing asexually into two perfectly formed and identical individuals to see protoplasm at work in this manner. It manufactures these elaborate structures, and this can only be by virtue of its chemical constitution. How it comes about we do not know, but there is the fact that specific protoplasm in these protozoa produces specific structures. I maintain that the structures must obey the same laws as the chemical complexes forming the protoplasm which builds the structures. It will be not only the physiology of these early forms but the morphology which will modify itself to suit changing environments, in other words, will adapt itself. That is, as Berg said (1926, p. 8), "Purposive structure . . . is a fundamental property of the living being".

Inheritance in these earliest organisms with body form—let us take the bacteria for examples—must have been entirely through the protoplasm. There is no suggestion of sexual reproduction—it is simply asexual—so that if an individual modifies itself through changed conditions it divides into two daughter individuals which are also modified to suit the new environment. This is admirably discussed

by Hinshelwood (1949, p. 154) but where I maintain he has gone wrong is in looking for a gene mechanism at this level. Bacteria are not unicellular organisms as they are usually referred to but non-cellular animals as Dobell (1911) established many years ago. As I have pointed out earlier in this essay it is not until the evolution of the cellular structure, that is, above the protozoan level, that there is any true cell, mitosis, chromosome or sexual reproduction. It is therefore not until this level that we have any right to look to a gene mechanism to explain inheritance.

It is the type of inheritance which has evolved up to this level which I maintain is of such vital importance. How many aeons passed between the first appearance of life on this earth and the first cellular organism we cannot say, but during all that time I can see no reason for assuming that inheritance and hence evolution was through any other means than through the whole organism and more specifically through their particular protoplasms, and this evolution as I have tried to show must have been purposive.

Johannsen writing in 1923 (p. 138) and referring to the type of organism used in Mendelian experiments, stated that it must be considered as "a great central 'something'" in addition "to all the separable, mendelising characters" (Russell, 1930, p. 69). But then he qualified his 'something' by adding the words "as yet not divisible into separate factors" and this, to my mind, spoils the whole of his conception. There is no reason to suppose that this "great central 'something'", the existence of which Johannsen postulated as a result of most distinguished work on genetics, is also particulate like the gene complex of which he was the parent. It represents according to my views the fundamental property of living matter, of protoplasm whether amorphous or organised, to adjust itself to changes in the environment always in the manner optimum for its survival.

Is there any reason to suppose that when cells appeared with all their complexities and their gene complex inheritance, this organismal type of inheritance disappeared? As I see it both types of inheritance have persisted to the present day. The first organismal type which I have tried to show must be a concomitant of organised living forms is responsible for the functional adaptations—for the directiveness in evolution of Wood Jones or for the nomogenesis of Berg and for Lamarckian inheritance in its true sense. The second gene complex type which must have come in so much later is that which deals with chance variations of existing structures and may or may not lead to characters of functional significance.

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OBSERVATIONS ON FLYING AND FLIGHTLESS WATER BEETLES.

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(With Plate 1 and 12 Text-figures.)

[Read 20 January 1955.]

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INTRODUCTION.

In 1952 I recorded some observations on the capacity for flight of water beetles. Many species were found to fly well but others were incapable of flight. Dissection showed that in the flying species the fibrous muscles of flight were fully developed in all the individuals examined, but in the flightless species these muscles were abnormal or absent. In such species the metathorax showed various modifications, and sometimes the wings were reduced in size. In other species the condition of the flight muscles was found to be variable in different individuals, some being capable of flight and others flightless.

My investigations have been continued and some of the results are included in a paper, now awaiting publication, dealing with the flight capacity of various species found in Scotland, which also occur in the Western Scottish Islands. The present paper is based on observations on other species not yet dealt with or only briefly mentioned (1952) and it includes an account of the structural differences observed between a flying and a flightless water beetle of the genus *Agabus*.

My best thanks are due to the following entomologists who have so generously sent me specimens for dissection—recorded under their initials in the following notes: Mr. S. E. Allen, Professor F. Balfour-Browne, Mr. E. S. Brown, Mr. L. Christie, Mr. F. D. Goodliffe, Dr. F. Guignot, Dr. H. B. N. Hynes, the Rev. T. B. Kitchen, Professor C. H. Lindroth, Mr. A. Smith, the Rev. E. J. Pearce, Dr. R. Richter and Dr. F. N. Young.

I am grateful to Miss Edith Evans of the Royal Entomological Society of London for her kind help in supplying me with literature and to the staff of the University Library, St. Andrews, for similar valued assistance, also to the late Mr. T. G. Lockie, of the Natural History Department of St. Andrews University for his skill in taking the photo-micrographs.

SPECIES WITH WELL-DEVELOPED WINGS AND FLIGHT MUSCLES.

It is well known that water beetles are sometimes attracted to light and it is of obvious interest for this investigation to include all records of beetles so captured. Scott (1953) recorded a large flight of water beetles, principally *Hydrobius fuscipes*, at light near Weymouth in July 1952, during a hot, dry spell. I found *H. fuscipes* to be one of the most ready fliers in tests which I carried out at St. Andrews (Jackson 1952). The beetles flew both by day and night, and all those I dissected had fully developed flight muscles.

Similar evidence of the attraction of water beetles to light in July 1952 was supplied to me by the late Dr. K. G. Blair from the Isle of Wight. He used a mercury vapour lamp in his study and left it on all evening with the windows open. He wrote on 28 November 1952 that 21 July was a wonderful night for beetles at light, they were in swarms. Water beetles were *Colymbetes fuscus*, *Copelatus haemorrhoidalis* (*agilis*), *Gyrinus natator* and *Hydrobius fuscipes*, the last species in numbers, the rest in singletons. He stated that *H. fuscipes* was a fairly frequent visitor and *Helophorus minutus* was taken on 6 May 1949.

Further records included in the following notes show that in some species natural flight may occur on mild days even in winter. Early in February 1954 I collected specimens of *Agabus bipustulatus* L. from a frozen pool near St. Andrews, after breaking the ice an inch thick. When tested the same evening in a warm room one beetle flew within half an hour.

When testing the beetles for flight I placed them in a large, shallow tin, lined with cardboard, with sides sufficiently steep and slippery to prevent their climbing out. Very noticeable, especially in the larger species, is the buzzing or humming which usually precedes flight. I have watched a *Dytiscus semisulcatus* Müll. getting ready to fly and the humming lasted quite five minutes before the elytra parted and the beetle flew. In smaller beetles the noise is less noticeable but I have heard it even in *Laccophilus minutus*. I have noticed with *Graphoderus cinereus* and *Agabus bipustulatus* that during the buzzing the elytra vibrate, but with the latter species I could only detect the movement under a dissecting microscope. Wesenberg-Lund (1912, 1943) and Korschelt (1924) state that during the humming the whole insect vibrates and that the tracheal system, and especially the large air sacs in the meso- and metathorax, fill with air. Wesenberg-Lund thinks that the sound may be caused by the vibration of the spiracles, especially of the first pair, but he quotes Griffini as attributing the sound to the hind wings.

Hygrobia hermanni F.

Warm weather would appear to be the deciding factor in stimulating this species to fly. Yorkshire specimens, obtained in April 1952 (A.S.), were tested for flight at St. Andrews for several hours on various occasions, in sunshine, both indoors and out of doors, and in a warm room at night, but none flew until 15 May, a warm day, when five exposed to sunshine took off within five minutes.

Agabus didymus Ol.

Two specimens have been dissected with full-sized wings and normal flight muscles, one without data (F.B.B.) and one which I took in Askham Bog, Yorkshire, in April 1952.

Agabus conspersus Marsh.

Four specimens without data (F.B.B.) had fully developed flight muscles, and six specimens collected in south-east Yorkshire in July 1954 flew in sunshine within six minutes of testing.

Agabus melanarius Aubé.

This rare and local species is capable of flight. Dried specimens from the south of England (F.D.G.) showed well-preserved normal flight muscles, though examined several months after capture, and living specimens sent to St. Andrews in April 1953 made repeated short flights. On a warm, sunny day in April 1954 Goodliffe showed me the habitat of this species. I removed a few specimens to dry ground near their pool and in a few minutes several flew away.

Ilybius ater Deg.

Specimens have been sent me (L.C.) from the south of England taken at light in July 1951 (H. D. Swain); August 1954 (R. L. Ford), and September 1953 (C. F. Astbury). A. A. Allen records (1953 c) taking a specimen on the wing on 10 May 1951. He informs me that it was a female not fully hardened and that it was flying during a sunny interval on a very warm and close afternoon. All the specimens I have dissected from Fife and the south of England had fully developed flight muscles.

Ilybius aenescens Thoms.

Specimens from the Scottish Highlands (D.J.J.) and from Dorsetshire (F.D.G.) had normal flight muscles and Goodliffe netted one flying into a pond in Surrey on 11 April 1954.

Ilybius subaeneus Er.

Specimens from Yorkshire (T.B.K.) flew readily when tested at St. Andrews and had the flight muscles very well developed.

Copelatus haemorrhoidalis F. (*agilis* F.).

Already recorded as taken at light by Scott (1953) and noted above as so captured by Blair. Specimens sent from Hampshire (F.D.G.) had normal flight muscles and others flew readily when tested.

Rantus notatus F. (*frontalis* Marsh.).

Specimens I took at Morton Loch in Fife in August 1952 flew readily when tested.

Rantus pulverosus Steph.

A male was taken at light at Putney by Swain in July 1951 (L.C.), and a female was captured at Lund, Sweden, flying to light on 8 July 1954 (C.H.L.).

Rantus bistriatus Bergstr.

A male, collected near St. Andrews, flew when tested on 3 September 1951. S. E. Allen has noted (1953) the flight of this species to a pond in Hampshire on a very warm day in February, and he suggests that the beetles were returning from hibernating quarters in a sheltered bog nearby. He records the flight during a very hot spell in July 1952 of a male *Hydaticus seminger* Deg. in the same locality.

Graphoderus cinereus L.

The discovery of this rare species in Hampshire by S. E. Allen is recorded by A. A. Allen (1953 a, b). Two spirit specimens sent to me (S.E.A.) had fully developed

flight muscles. The metatergum of one was mounted. It is strongly sclerotic with well-developed prephragma and postphragma for the support of the median meta-thoracic muscles of flight, and the discs of the pleural wing muscles are large. Six living specimens received in May 1953 (S.E.A.) eventually flew when tested, five taking off on a warm, sunny afternoon on 22 May and the sixth flew at a later date. They are very strong fliers, two rose straight up from the testing dish flying upwards towards the sun and soon disappeared from view.

Dytiscus circumflexus F.

In February 1954 Christie sent me a male and female, the latter still alive, which had been taken in a mercury vapour light-trap by A. J. Dewick at Curry Farm, Bradwell-on-Sea, Essex, on the night of 22-23 February. On the preceding night 25 *Dytiscus* were taken in the trap but were not more nearly identified. Dewick informs me that he also took 22 *Dytiscus* in the trap on the night of 17-18 January 1953. It is interesting to find that Huggins (1954) records the capture of nearly 40 *Dytiscus marginalis* females in a light-trap at Hockley (Essex) on the same night (17-18 January 1953) and he mentions that it was an unusually hot one for the time of year. It is clear that these *Dytiscus* species must be extremely active on mild nights in winter. I found that the female *D. circumflexus* had well-developed ovaries but no ripe ova, the largest measuring 2.3 mm. : the size of the egg of *D. marginalis* when ready to lay is given by Korschelt (1924) as 7 mm. S. E. Allen recorded (1953) *D. circumflexus* in cop. below thick ice in January.

COMPARISON OF FLIGHTLESS *AGABUS UNDULATUS* WITH A FLYING *AGABUS*

The Species Compared.

Agabus undulatus Schr. is widely distributed in northern and central Europe and Blunck (1913) stated that in Schleswig Holstein it was rarely absent from small to medium-sized ponds, yet its distribution in England is limited to certain fen districts. It has not been found in Scotland or Ireland. Blunck noted that, though abundant in the spring, it was only sparingly present in the same ponds at other times of the year. He believes that it becomes adult in June and that the beetles remain in their pupal cells during the summer when their ponds dry up, and do not enter the water until the autumn rains commence, or even later. Since Balfour-Browne (1950) collected 60 newly emerged specimens in Yorkshire, at Chaloner's Whins, in August 1906, and I have taken both old and newly emerged specimens there, and in the nearby Askham Bog on 12 July 1953, the beetles must remain active as long as the water holds out. All the specimens I have dissected, 23, came from this area. I have dissected specimens of varying ages, from soft newly emerged specimens to those with fully mature reproductive organs, and all were flightless. Four specimens from Vacluse in the south of France (F.G.) showed the same flightless characteristics as the English specimens.

Agabus chalconatus Panz. has been chosen as an example of a flying *Agabus*, since small specimens of this species are equal in size to large specimens of the flightless* *Agabus undulatus* and so are convenient for comparison. *A. chalconatus* is widely distributed in Europe and throughout the British Isles. It occurs in two forms, the type form which appears to be restricted to the southern part of Great Britain (Balfour-Browne, 1950) and var. *melanocornis* Zimm. which occurs also in Scotland. I have dissected over 40 specimens of *chalconatus*, including the type form (E.S.B.), and var. *melanocornis*, and all had normal flight muscles; moreover I have netted a specimen on the wing in Inverness-shire, on 5 October 1945.

The following account would probably apply equally well to any other flying *Agabus* and it has been drawn up after a detailed study of both *chalconatus* and

* In using the word flightless in connection with a species I intend to imply that all specimens I have so far dissected of that species have been without normal flight muscles, and have shown corresponding modifications of the skeletal parts.

bipustulatus. The latter species is very common and widely distributed and a ready flier. I have dissected over 100 specimens of *bipustulatus* and have found all to have normal flight muscles.

The Flight Muscles.

The Normal Flight muscles.

An excellent account of the metathoracic muscles of *Dytiscus marginalis* has been given by Bauer (1910) and is included in Korschelt's monograph of this species (1923). As far as the indirect flight muscles are concerned it agrees in all essentials with the position of the muscles in *Agabus*.

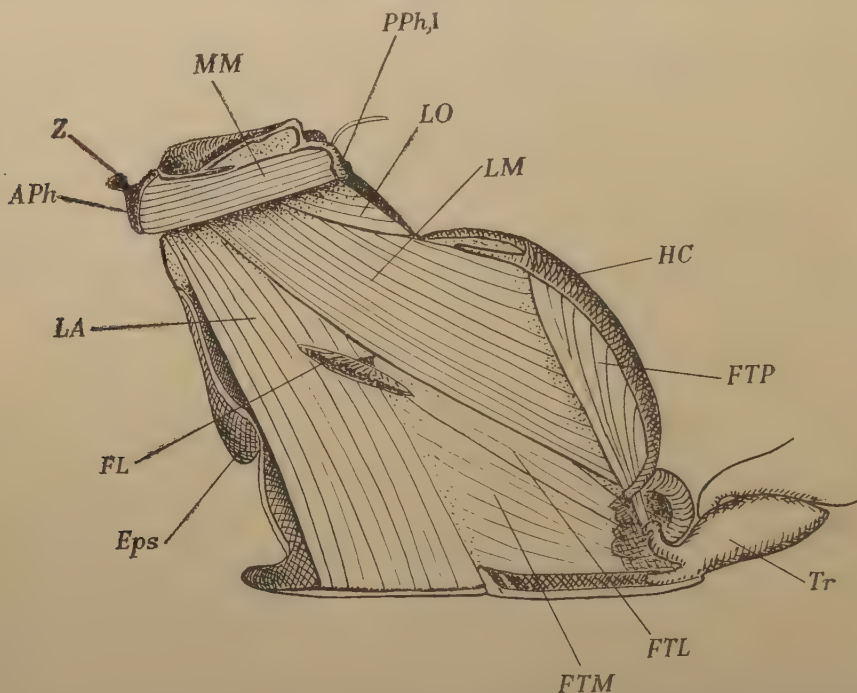


FIG. 1.—*Agabus bipustulatus* L. Longitudinal vertical section of the metathorax in the median plane $\times 18.3$. The furca (the metasternal apophysis) with its attached extensor trochanteris muscles has been cut away at the base to expose the dorso-ventral indirect flight muscles. [For explanation of lettering see p. 41.]

To examine the flight musculature it is convenient to cut the metathorax in half longitudinally and then to cut away the metasternal apophysis (the furca) which bears the principal extensor trochanter muscles. The indirect flight muscles are thus laid bare on each side and are very conspicuous (fig. 1). They are situated in two planes, longitudinal and vertical. The longitudinal dorsal muscles, which in Dytiscidae are comparatively short, are usually believed to cause the arching of the tergum and the lowering of the wings, while the dorso-ventral muscles bring about the depression of the tergum and the raising of the wings.* In *Agabus* the dorsal muscles consist of the median longitudinal muscles (*musculus metathoracis medianus* of Bauer) and a pair of lateral oblique muscles (*musculus lateralis metathoracis posterior*). The dorso-ventral muscles comprise two pairs of very large

* Boettiger & Furshpan (1952) disagree with the accepted theory of the cause of the downward movement of the wings. They have studied the mechanics of flight in flies by exposing them to the fumes of CCl_4 , whereby the wings can be 'frozen' in the up or down position, and they consider that the change in direction of the lateral force necessary to wing movement is produced not by alternate flattening and arching of the notum, but by the action of the 'scutellar lever'.

muscles, the *lateralis metathoracis anterior*, an almost vertical muscle going from the anterior lateral area of the scutum to the sternum, and the *lateralis metathoracis medius* inserted on the scutum, between the *lateralis anterior* and the lateral oblique dorsal muscle, and slanting downwards and backwards to the hind coxal fold (fig. 1, L.M.). By removing these dorso-ventral muscles the pleural wing muscles and the flexor trochanter muscles are exposed (fig. 2) lying at the side of the thorax.

The pleural wing muscles (fig. 2) consist of the *extensor alae anterior*, inserted in the basalar disc, and the *extensor alae posterior*, inserted in the subalar disc. The *extensor alae anterior* consists of two bundles of unequal length, the longer, anterior one having its origin on the sternum and the shorter posterior one lying parallel with the upper part of the other and arising from upper surface of the anterior coxal fold, a ledge like apodeme. The *extensor alae posterior* is a single large bundle originating in the hind coxal fold. Since the basalar and subalar discs are closely connected with the wing base, the large muscles inserted in these discs have direct action on the movement of the wings as shown by Snodgrass (1935), and so are usually termed 'direct' flight muscles.

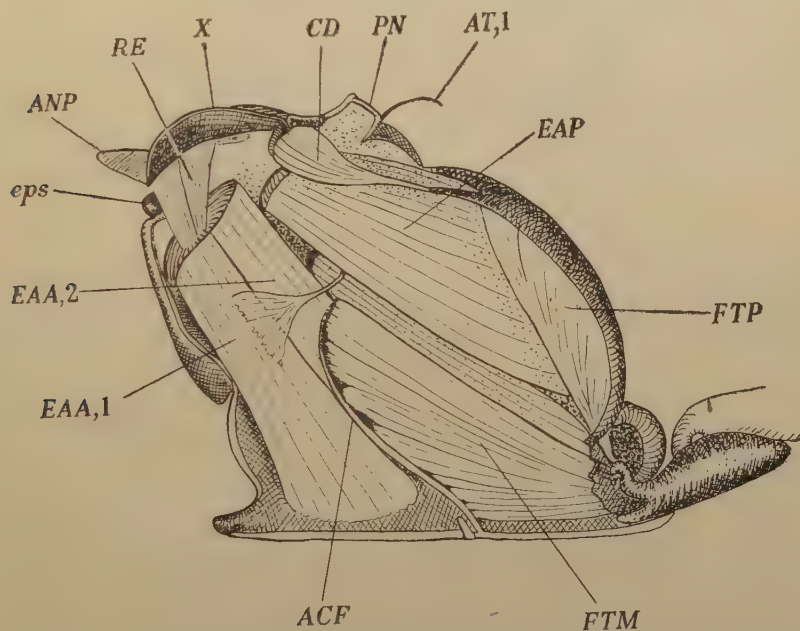


FIG. 2.—Same as fig. 1, but the dorso-ventral flight muscles have been removed to expose the pleural wing muscles, and the metatergum has been cut back to its extreme lateral edge. To simplify the drawing no tracheae are shown, nor the second spiracle which is situated at the left upper corner at the front edge of the basalar disc.

All the flight muscles already mentioned are of the fibrous type and it is only the fibrous flight muscles which show marked reduction or are absent in the flightless beetles. In a freshly killed beetle the fibrous muscles are cream coloured, contrasting with the tubular leg muscles which are of a glistening white, but in specimens long preserved in alcohol all the muscles appear yellowish. Histologically the fibrous muscles are readily distinguishable from the tubular muscles and are of very characteristic appearance, consisting of closely parallel fibres showing very fine cross-striation and with small nuclei occurring in rows, while the fibres of the tubular muscles usually converge at one end and are more coarsely cross-striated with larger nuclei lying in a row in the centre of each fibre.

Székey (1947) has made very interesting observations on the character of cross-striation and its relation to the work performed by the muscle. He studied a mandibular muscle, a leg muscle and an indirect dorso-ventral flight muscle in various insects, and he found that the indirect flight muscles possessed the lowest myomeres and worked at a higher frequency, and he concludes that the frequency of the muscle contraction and the height of the myomeres are inversely proportional: in other words the higher the demand on the muscle the lower are the myomeres. Therefore, the fine cross-striation of the fibrous flight muscles of *Agabus* will be directly related to the work required to keep the beetle in flight.

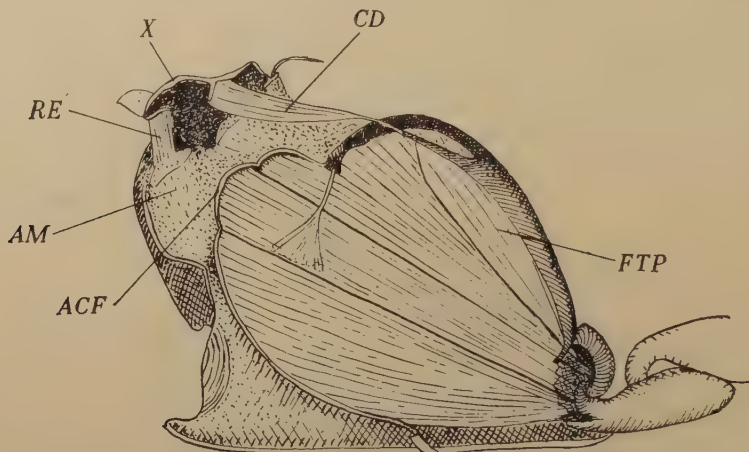


FIG. 3.—*Agabus labiatus* Brahm. Section of the metathorax in the same position as in Fig. 2, but magnified 27 to show the greatly developed *flexor trochanteris* muscles. Normal flight muscles are absent, but traces of abnormal flight muscles in the fat body are shown coming from the basalar and subalar discs. Fat body is indicated by irregular dotting.

The fibrous flight muscles of *Agabus* readily split up into the fibres or groups of fibres which compose them. The fibres vary in number according to the size of the muscle, over three hundred have been counted in one of the larger muscles (the *posterior extensor alae*) of *bipustulatus*, and this number is probably an underestimate, as even when the muscle is teased apart all the fibres do not separate. Morison (1927–28) found that the average number of fibres in the longitudinal muscles of the honey bee was 149. In *bipustulatus* the fibres vary in size from 30 to 50 μ in fixed material and from 60 to 90 μ in fresh muscle examined in 0.75 salt solution. It was noticed that in the flight muscles of a newly emerged *bipustulatus* (the specimen had flown) the fibres were smaller, 30 to 39 μ in Carnoy fixed material, and the nuclei were very numerous. An increased number of nuclei in the flight muscles of young weevils was also noted in *Sitona lineatus* (Jackson, 1933). The appearance of longitudinal striation in the fibre (Pl. 1, fig. 13) is due to the numerous fibrils or sarcostyles. Both the fibrous and the tubular muscles are doubly refractile when viewed with polarized light with crossed Nicols, but the abnormal flight muscles are not, neither the very minute ones found in *Agabus undulatus* nor those of almost 'intermediate' state found in some examples of *A. paludosus* F. and *A. guttatus* Payk; but small pieces of tubular muscle accidentally mounted with these abnormal flight muscles give a brilliant contrast and are proof that the fixative or mountant is not responsible for the non-luminosity of the abnormal flight muscles.

In addition to the large fibrous flight muscles already mentioned there are very small 'direct' tubular muscles at the wing base which are concerned in movements of the wing, the largest being the *musculus flexor alae*. The position of these muscles as described by Bauer in *Dytiscus* are, with one exception, very similar to what I have

found in *Agabus*. The exception is the *relaxator extensoris* which I find goes from the upper edge of the basalar disc to the lateral edge of the prescutum and not to the 'Chitinplatten am Flügelgrunde' as Bauer records for *Dytiscus*. There is little, if any, difference in the size of these small muscles in the beetles in which the fibrous flight muscles are reduced, and they usually show normal striation. A larger muscle, the *coxo-dorsalis metathoracis*, a gleaming white muscle of tubular type (fig. 2, C D.) goes by a long tendon from the spur of the hind coxal fold to a lateral projection of the scutum near the wing base, which I have designated the median notal process (fig. 4, D). Bauer considers this to be a leg muscle which, owing to the fixation of the coxa has ceased to function as such, and acts instead as a raiser of the wing. I have found this muscle to be as well developed in flightless *Colymbetines* as in those capable of flight: it is even well developed in brachypterous *Noterus crassicornis* Müll.* in which flight is out of the question. A probably homologous muscle was observed in the Hydrophilid, *Anacaena globulus* Payk. (Jackson, 1952). This small beetle, though without fibrous flight muscles (74 specimens have now been dissected), was often seen when falling on its back (during tests for flight), to part its elytra and spread its hind wings in its efforts to get up, and I believe that the action of this muscle caused the extension of the wing. Specimens of *Agabus uliginosus* L., without normal flight muscles, behaved in exactly the same way, and they had the *coxo-dorsalis* muscle very well developed. By pressing with a needle on the median notal process in a freshly killed specimen of *uliginosus* I found the wing rose up. It is difficult to understand what function this muscle can have in the normal life of a flightless beetle unless it is used in respiration. I have found it well developed in the Carabid *Feronia nigra* Schall. with reduced wings.

The Abnormal Flight Muscles.

In most of the *A. undulatus* dissected I failed to find any flight muscles; in some, by staining and mounting the fat body beneath the metatergum, small and slender lineal groups of extremely minute fibres with numerous elongated nuclei were visible embedded in the fat. The minute size of these abnormal muscles is shown (Pl. 1, fig. 14) where the width of a whole muscle is not as large as a single fibre of normal flight muscle of *A. bipustulatus* (Pl. 1, fig. 13). In a few specimens the abnormal flight muscles were larger, and in one 'soft' (i.e. newly emerged) specimen the fibres reached a thickness of from 5 to 6 μ . In such abnormal muscles the minute fibres lie apart and are irregularly spaced, with numerous tracheae, tracheoles and fat cells between them, and the fibres show no cross-striation.

The abnormal flight muscles result, I believe, from an arrest of development at an early stage. Breed (1903), who has studied the development of the muscles in the beetle, *Thymalus marginicollis* Chev., found that the majority of the wing muscles appeared to be transformed larval muscles, and he notes the presence of many elongated nuclei and numerous chains of nuclei in the developing muscles in the pupa. I found that in newly emerged weevils of *Sitona lineatus* L., an excellent flier, the histology of the flight muscles resembled that of the abnormal flight muscles which occur in some mature specimens of *S. hispidulus* F., but the normal structure was usually attained in less than a month after emergence (Jackson 1933). In 'soft' specimens of flying water beetles I found the flight muscles had already attained almost the normal structure, and in the flightless specimens the development of these muscles is probably arrested in the pupa at an early stage.

The Elytral Muscles.

I have not made a comparative study of the mesothoracic muscles in the flying and flightless beetles. I find that all the muscles of the mesothorax are of tubular type and, from a casual inspection, they look just as well developed in the flightless as in the normal beetles, and this was what I found in *Sitona hispidulus* F. (1928).

* This is the name by which the smaller species, formerly called *N. clavicornis* Deg. by British writers, should now be known. Jackson, 1954, *Ent. Gaz.* 5, 63.

The Metathorax.

The following description refers principally to those parts of the metathorax which show modification in the flightless beetles.

In a Flying Agabus.

The *Metatergum* is darkly sclerotic. It has a compact appearance both in *chalconatus* and *bipustulatus* and is longer than the first abdominal tergite. The prephragma and postphragma are well developed to give insertion to the median longitudinal muscles. To the expanded lateral area of the postphragma (fig. 4, P Ph, 2) the posterior ends of the lateral oblique dorsal muscles are attached. The internal ridges of the metatergum are prominent and consist of the V-shaped ridge of the scutellum, and, anterior to this the oblique intrascutal ridge which divides the scutum into anterior and posterior parts. The intrascutal ridge projects downwards as a shelf, and, in the angle between it and the V-shaped ridge, the lateral oblique muscles are inserted. Above this ridge the anterior lateral part of the scutum gives insertion to the dorso-ventral muscles as already described. At the side of the metatergum, lying between the anterior and posterior notal wing processes which articulate with the first and third axillary sclerites of the wing, is the strongly developed median notal process (fig. 4, D) to which the *musculus coxo-dorsalis* is attached.

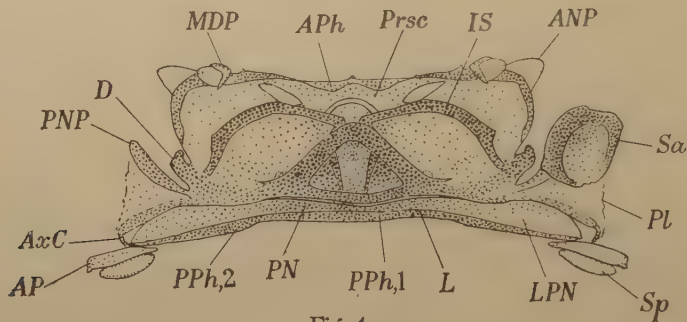


Fig. 4

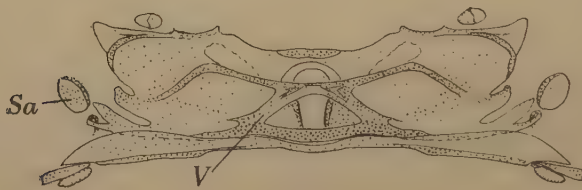


Fig. 5

FIG. 4.—*Agabus chalconatus* Panz. Metatergum, internal view. The subalar disc of the pleuron, lying in the transparent pleural membrane, has been left *in situ* on the right of the figure, but has been omitted on the other side to show the postnotal wing process which articulates with the base of the third axillary sclerite of the wing. From a mature male with normal flight muscles, $\times 17$.

FIG. 5.—*A. undulatus* Schr. Metatergum, internal view, and subalar discs of a female collected Askham Bog, without flight muscles, $\times 17$.

The only parts of the *Metapleuron* to which I need refer are the discs of the pleural wing muscles. The position of these discs is shown in my previous paper (1952, fig. 1). The anterior muscle disc, the basalar disc, is attached to the strut-like process, the basalar, which articulates dorsally with the head of the costal vein of the wing and basally it is attached to the episternum. The basalar disc and the basalar, together constitute the anterior or episternal epipleurite, while the posterior disc, the subalar disc, is the epimeral epipleurite. Since the pleural wing muscles

are fully developed in a flying *Agabus*, these discs are very large in a fully hardened beetle and darkly sclerotic. The subalar disc of one side is shown (fig. 4, Sa).

The *Sternum* in both *chalconatus* and *bipustulatus* has wide metasternal 'wings' (fig. 9) and relatively shorter post-coxae than in *undulatus*, and, in conformity with this, the flexor trochanter muscles of the hind legs are shorter since they arise principally from the anterior coxal fold, an apodeme projecting from the anterior wall of the coxa.

In A. undulatus.

The metatergum is greatly modified (fig. 5). It is a little shorter than the first abdominal tergite and considerably shorter than the metatergum of a flying species. The prephragma is less prominent and the postphragma is reduced except where it gives insertion to tubular body muscles. The whole tergum is less sclerotic and less arched than in *chalconatus* and the internal ridges are weakly developed. The discs of the pleural flight muscles are quite small. The sternum is characterized by its narrow metasternal 'wings' (fig. 10) and the proportionately large post-coxae, and the flexor trochanter muscles are greatly developed, suggesting a greater activity of the hind legs.

There is no doubt that in this species and also in *A. labiatus* (fig. 3) and the related *Platambus maculatus* (in both of which the metasternal wings are narrow), the flexor muscles of the hind legs have been developed to the exclusion of the flight muscles, for the flexor muscles are much longer in these species than in *bipustulatus*, *chalconatus* and other species with well developed flight muscles and wide metasternal wings. The increased size of the flexor trochanter muscles in these flightless species is due partly to the greater size of the coxa and partly to the increased size of the anterior coxal fold which is greatly produced anteriorly, so that, if one views the metasternum from its external aspect, after removing the met-episternum, the anterior part of this apodeme projects conspicuously (fig. 10, ACF). In *chalconatus* and *bipustulatus* on the other hand this apodeme forms a narrow ledge, and only in one place is it produced into a pointed process which projects beyond the edge of the metasternal wing (fig. 9, ACF) and supports the longest of the flexor muscles. These apodemes are only fully developed in hardened specimens, in 'soft' specimens they are smaller and unpigmented though the flexor muscles are well developed.

It is difficult to homologize the trochanter muscles lying at the side of the coxa with those described by Bauer in *Dytiscus*. They all cause movement of the hind leg if pulled. In a flying *Agabus* these muscles are grouped mainly in the anterior part of the post-coxa (fig. 2) and do not extend into the hollow of the hind coxal fold as this is occupied by the *extensor alae posterior*.

In the genus *Agabus* I have found that other species which have wide metasternal 'wings' have fully developed flight muscles, e.g. *nebulosus* Forst., *conspersus*, *biguttatus* Ol. and *melanarius*. In some species in which most of the specimens I have dissected have been without normal flight muscles, such as *affinis* Payk., *paludosus* F. and *arcticus* Payk., the 'wings' are of intermediate size. *A. guttatus* Payk., however is an exception since the 'wings' are wide and the flight muscles abnormal. Two large flight muscles, the *lateralis anterior* and the *extensor alae anterior*, arise from the metasternum, and I think it is possible that, a reduced sternum in the genus *Agabus* (and also perhaps in *Deronectes* and *Plybius*) may be correlated with reduced flight muscles. In some other genera species with narrow metasternal 'wings' have normal flight muscles, as in *Copelatus*, *Graphoderus* and *Acilius*, but until the musculature has been studied in each genus no generalizations can be made. In *Copelatus haemorrhoidalis* the sternum itself is wide, and in *Acilius sulcatus* I find the pleural wing muscles consist of two large bundles, instead of three, and the flexor trochanter muscles are relatively much less developed, the posterior part of the large post-coxa being occupied by the *extensor alae posterior*.

It is interesting to find that Balfour-Browne (1950) concludes that the evolutionary trend, in Colymbetines has been towards narrower metasternal 'wings'.

The Abdominal Tergites.

In *chalconatus* the abdominal tergites are brown and the pygidium is dark brown, but in other *Agabus* which fly well the tergites are frequently brilliantly iridescent as is well seen in *A. bipustulatus*, in which the first three segments are of a brilliant bluish green and the next two or three show these colours to a lesser extent. The iridescent tergites show innumerable minute and irregular darkly sclerotic ridges, interspersed with small bristles; the brown tergites of *chalconatus* have the ridges paler and the surface smoother and the anterior segments are more densely covered with minute bristles. The last three tergites in all species examined are beset with bristles, those on the propygidium and pygidium being very large and directed backwards. It seems probable that the sculptured and bristle-beset tergites will not only protect the abdomen of the beetle from desiccation during flight, but, helped by the oily secretions of the dermal glands, will repel the water when the beetle dives in after flying, if the elytra are not entirely closed.

In *undulatus* as in other flightless species, such as *A. labiatus* and *Platambus maculatus*, the anterior tergites are pale and membranous, less ridged and with fewer bristles, than in the species with normal flight muscles. A dark spot is conspicuous on the sides of the first tergite and sometimes a smaller one on the second, and these mark the attachment of muscles arising from the hind coxal fold and believed to function in respiration (Korschelt, 1923). Pale tergites are not always characteristic of flightless beetles, as, in *Ilybius fuliginosus*, which flies well and has a light coloured under surface, the tergites are pale, but they are beset with small bristles. In *Noterus*, and some flightless Hydroporini, the abdominal tergites may be sclerotised, but in such species the elytra are more than usually transparent.

The Spiracles.

There are two pairs of thoracic spiracles and eight pairs of abdominal spiracles. The first pair lies between the pro- and mesothorax, and no difference has been detected in its size in *chalconatus* as compared with *undulatus*. The second thoracic pair may be found by removing the mesothorax, when (if not torn off in the process) the large spiracle may be seen at each side of the metathorax, lying slantwise in front and between the prescutal muscle disc and the episternum. The first pair of abdominal spiracles is large (fig. 4, Sp.) and of oval shape, the remaining pairs are much smaller and circular.

In *undulatus* the second thoracic spiracle is only a little smaller than in *chalconatus*, but the first abdominal spiracle of *undulatus* was only half as large as that of *chalconatus* when two beetles of approximately the same size were compared. In five specimens of *undulatus* this spiracle varied in size from 0.25 to 0.3 mm., but in six *chalconatus* it varied from 0.44 to 0.54 mm. The other pairs of abdominal spiracles are similar in both species. I have observed a similar reduction in size of the first abdominal pair in other water beetles without normal flight muscles. These spiracles are closely applied to the ends of the postphragma, and Alt (1912) has shown that in *Dytiscus marginalis* the tracheae issuing from these spiracles go to the metathorax, supplying some of the principal leg and flight muscles. Rüschkamp (1927) observed that in Chrysomelids this third body spiracle, which he considers belongs functionally to the metathorax, is large in the flying species to provide the flight muscles with oxygen during action, but is reduced in size in the flightless species.

The Wings and the Intercubital Plate.

The wings of *undulatus* are much smaller than the wings of *chalconatus* and this is easily seen by comparing beetles of the same size (figs. 6 and 7) and it is the apical region of the wing which is most reduced. There is, however, one area of the wing which shows no reduction. This is the broad dark band, called by Goodliffe (1939) the intercubital plate, which lies between the distal parts of the cubital vein and abuts on the hind margin (fig. 6, IP.). In *undulatus* it is composed of minute round knobs which are very closely placed on the dorsal surface of the wing. At

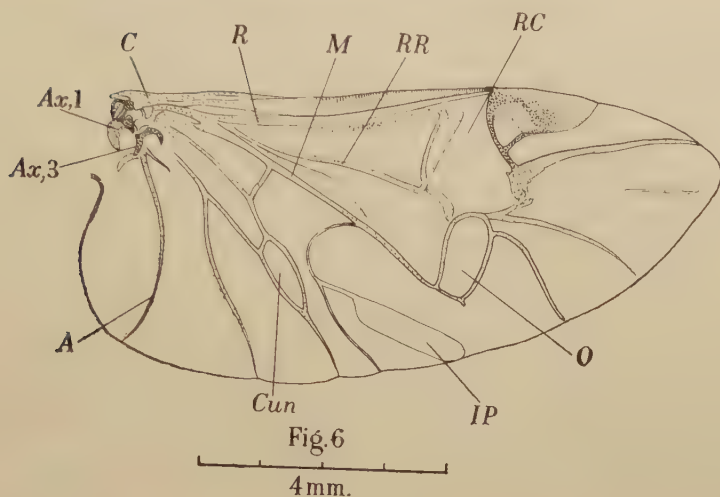


Fig. 7

FIG. 6.—*A. chalconatus* Panz. Wing, $\times 8.25$. Nomenclature of wing veins according to Guignot (1933).

FIG. 7.—*A. undulatus*. Wing $\times 8.25$ from a beetle of the same size as *A. chalconatus*.

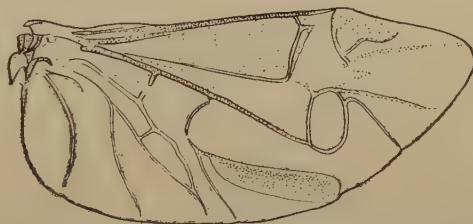


FIG. 8. *Platambus macalatus* wing $\times 8.25$ from a beetle of the same size as *A. chalconatus*.

the margin of the band the knobs are produced into bristles, stouter than the bristles which cover the rest of the wing membrane, and this suggests that the knobs are homologous with the bases of insertion of the bristles. There is an ill-defined pale central line in which the knobs are smaller and spaced further apart. The under-surface of the wing below bears the usual small bristles but they are shorter than on the rest of the wing. When the wings are folded, one wing crosses over the other, and these bands lie in a straight line along the mid-dorsal area of the abdomen, one above the other, the wing being transversely folded at the apex of the band. The sutural regions of both elytra rest on the band of the uppermost wing, the pale central line coinciding with the junction of the elytra. A longitudinal strip on each elytron beside the suture is shagreened where it meets the wing, and, in the elytron of a 'soft', newly emerged, *A. undulatus* this is seen to be due to the presence of

minute, closely placed, knob-like processes. Similar processes occur along the outer margin of the elytra where they interact with a shagreened area on the abdominal pleurites.

These intercubital plates are well known to systematists as a characteristic of the Dytiscid wing. I have found them in all the Dytiscidae I have examined with the exception of *Hyphydrus ovatus* L. (Heberdey, 1938, states that they are also absent in *Hydrovatus*), but they are very variable in their degree of development in different species and the elements composing them also vary in shape. Arrow (1924) and Marcu (1936) believed them to be stridulating areas interacting with the elytra. Some writers believe that certain Dytiscidae stridulate, but Dudich (1921) was unable to confirm this. I have kept many species alive for weeks in my laboratory but I have only heard stridulation, and that frequently, with *Agabus affinis*, in May and June, a vibratory note surprisingly loud for this small beetle, repeated in quick succession four or five times and coming from the receptacle in which I had placed both sexes of this species. The male of *affinis* possesses a file on each side of the apparent third (true fourth) sternum of the abdomen, and Scholz (1932) quotes V. Hansen as stating that the vibration is produced by the male rubbing this file with the edge of its hind femora when mounted on the female immediately before copulation.

An entirely different view of the function of the intercubital plate is put forward by Heberdey (1938) in a very interesting paper. He names this structure the 'Katastigma' or 'Hinterrandsmal', and he has observed it, not only in Dytiscidae, but also in various families of the Polyphaga, in which, though it may vary in position according to the venation, its situation in the folded wing is constant. He has studied it principally in the Dytiscid, *Rantus punctatus*, Geoffr. He considers it to be one of several devices which serve to lock the elytra to the abdomen and to maintain the subelytral space, so important for the respiration and hydrostatics of Dytiscids. In land beetles he states that it is developed in forms which principally inhabit wood, fungi, vegetables or fruit, where there is danger of the spiracles becoming contaminated. He shows that the katastigma of whichever wing happens to be uppermost interlocks with the similarly roughened area on the elytral suture and so prevents the latter being moved out of position by external pressure.

It seemed to me at first doubtful whether the membranous hind wings could exert any such hold on the much harder elytra, but from a simple experiment I believe that Heberdey is right. If one forcibly removes one elytron with a needle or cuts it away with scissors, leaving the wing beneath it intact, the other elytron remains firmly in place, occupying one half of the katastigma, and one cannot raise it up without force. But if, with a fine needle, one pulls out the katastigma of both wings from under the closed elytron, the latter can be lifted easily. Sometimes a slight resistance may occur from another elytral 'lock', the shagreened area of the pleurites already referred to. This experiment works with various *Agabus*, *Rantus* and *Platambus*, provided they are freshly killed or preserved in spirit, but in newly emerged specimens the cuticle is too soft for the locking devices to work and the elytra come readily apart.

I have found the katastigma to be particularly well developed in *A. undulatus* and in other species in which the wings are reduced in size, such as *Platambus maculatus* L. (fig. 8) and *Ilybius fenestratus*, and the prominence of the katastigma, in these three species shows well in Goodliffe's photographs (1939, pl. II).

The katastigma is present even in the extremely reduced wing of *Agabus bifarius* Kirby, as was observed by Arrow (1924), and it shows also in Balfour-Browne's figure of the reduced wing of *A. maderensis* Woll. (1950). Its persistence in flightless forms despite the reduction of the other parts of the wing, emphasizes its importance in the aquatic life of the beetle. There can be no doubt that the katastigmatal 'lock' and the pleural 'lock', in addition to steadying the elytra against external pressure, will also have important hydrofuge properties, in sealing respectively the elytral suture and the sides of the posterior part of the abdomen. The small bristles on

the undersurface of the elytra at the apex and the profuse covering of bristles on the pygidium and propygidium already referred to, will also serve to repel the water during movements of the apex of the abdomen.

In beetles preparing for flight, Heberdey considers that the katastigma when present must be loosened by certain vibratory movements of the hind wings parallel to the long axis of the body, combined with a slow moving apart of the elytra. While watching *A. bipustulatus* getting ready to fly, I have noticed that during the buzzing already referred to, the tips of the hind wings are sometimes protruded and withdrawn, while the elytra make slight movements of parting and shutting. The extension and withdrawal of the tip of the abdomen, often seen before buzzing commences, may perhaps serve to unfold the wings.

The Wing Venation.

The venation of the wing of *Agabus undulatus* is strong. The degree of prominence of the venation shows much variation in the different Dytiscidae I have examined, both in normal and in reduced wings. In some of the latter the wing veins are dark, as in *undulatus*, in others, e.g. *Laccophilus hyalinus*, the veins are pale. Even in the same species the pigmentation of the wings varies and that irrespective of the age of the beetle. In newly emerged beetles which are still soft the wing veins are pale, and full pigmentation is usually achieved when the beetle is hard. The wing of *chalconatus* which I have figured has rather pale veins though it was from a mature specimen. Dunn (1951) found that the age of a Colorado beetle could be determined for at least fourteen days after emergence by the degree of pigmentation of the wings.

Comparison of A. undulatus with A. bifarius.

A. undulatus shows the greatest reduction of wings and of muscle supports that I have seen in any British Colymbetinae; *Platambus maculatus* L*, with a slightly larger wing coming next (fig. 8). It is interesting to compare these species with the brachypterous form of *Agabus bifarius* Kirby, an American species showing wing dimorphism (Leech, 1942). One specimen from Michigan (F.N.Y.), had the wings reduced to narrow slips. It had no trace of flight muscles and the metatergum is very similar in structure to that of *A. undulatus* and *P. maculatus* and the pleural discs are of the same small size. The similarity of the reduction of the metatergum and pleural discs in these three species, supports my view that, in the British species, the wings are useless for flight. Probably flight reduction is due to one or more mutations, and the reduced wing of *A. bifarius* has reached a further stage than in the two British species. I have not seen the wing of the macropterous form of *bifarius*, but if the figure of it given by Leech is drawn to the same scale as the reduced wing, then it is only a little longer than the elytron, just as in *Platambus*.

OBSERVATIONS ON OTHER FLIGHTLESS AND ' VARIABLE ' WATER BEETLES.

Agabus labiatus Brahm.

This species is widely distributed in northern and central Europe and occurs in Siberia. It has a scattered distribution in the British Isles and is extremely local. I have dissected forty specimens, twelve from North Hampshire, one from Elgin (R.R.), and the rest from Fife; many of the Fife specimens were carrying sub-elytral nematodes (Jackson, 1951). In all those dissected the flight muscles were abnormal or absent. Three specimens from Sweden (C.H.L.), and six which I collected in Denmark were also flightless. When present the abnormal muscles show a little better development than in most *undulatus*. They appear as whitish, semitransparent strands, and consist of very narrow parallel running fibres, 3 to 5 μ in diameter, with long nuclei which occupy nearly the width of the fibres, and tracheae and many tracheoles are present, the latter running

* Full particulars regarding my observations on this species have been given in another paper now awaiting publication. Over eighty specimens of *P. maculatus* from many parts of Britain have been dissected and all are flightless.

parallel with the fibres. The tracheoles show up clearly after fixation with v. Studnitz's (1936) chloral hydrate fixative (one part glycerine and six parts 10 per cent. chloral hydrate solution), when examined in glycerine. Occasionally the abnormal flight muscles may be larger, with fibres up to 12μ in diameter, and more crowded with elongated nuclei, but even these larger muscles show no cross-striation and are not doubly refractile in polarized light with crossed Nicols.

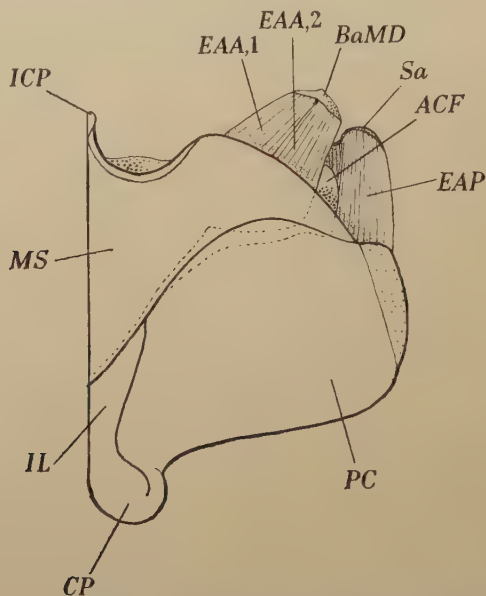


FIG. 9.—*A. chalconatus*. External view of left half of metasternum and post-coxa; the met-episternum has been removed, exposing the upper portion of the pleural wing muscles, $\times 20.25$.

The metatergum, pleural discs and wings all show characteristics intermediate in development between *chalconatus* and *undulatus*, but nearer to the reduced condition of *undulatus*. Several tests for flight were made, all unsuccessful. These beetles are active runners and the muscles of the hind legs as already mentioned are very well developed (fig. 3).

Agabus uliginosus L.

This is another local species with a limited range in Great Britain. It is not recorded from Ireland. It frequents bogs and brackish pools. It is widely distributed in northern and central Europe but Balfour-Browne (1950) states that it has not been recorded from Siberia or any part of the arctic region. I have received specimens from Dumfries (F. B. B.), and living beetles from Sully Island, Glamorgan (E. J. P.), which did not fly when tested. The Rev. E. J. Pearce informs me that he has taken this species there in a slightly brackish marsh for several years running, but only in the spring. I have dissected fourteen specimens. None had normal flight muscles, but, in most, abnormal flight muscles could be found. These were sometimes so surrounded with fat body that they showed a superficial resemblance in shape to normal flight muscles, but on mounting and examining with a compound microscope they were seen to be entirely different. The wings did not show reduction in size like *A. undulatus*, nor were the metatergum and pleural discs so much reduced, and the metasternal wings are wider. Four further specimens which I wished to retain for my collection were examined by lifting the elytra, when the pleural discs could be seen and these were of the same size as in the specimens dissected. It

would appear that this is a species in which reduction of the flying apparatus has not proceeded as far as in *A. undulatus*. It is interesting to note that Perkins (1862) found this species clinging to grass stems out of water in hot sun along a pond bank after a heavy shower of rain, and he states that he has "often found *A. maculatus* on the top of a stone wall evidently enjoying the blaze of a July sun". Is this perhaps a habit of species unable to fly? Mr. J. Balfour-Browne informs me that some years ago he was puzzled to notice in his aquaria that *A. labiatus* had a tendency to crawl up emergent stalks of grasses and spend several days sitting in one spot. They made no attempt to fly, so far as his observations went.

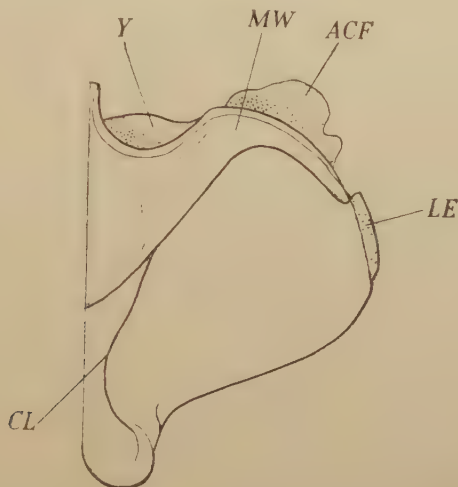


FIG. 10.—*A. undulatus*. External view of left half of metasternum and post-coxa: the met-episternum has been removed, exposing the upper edge of the anterior coxal fold. $\times 20\cdot25$. The unexposed part of the anterior coxal fold in this and in the preceding figure is indicated by a dotted line.

Laccophilus hyalinus Deg. compared with *L. minutus* L.

Laccophilus hyalinus occurs in almost the whole palaearctic region and has been taken in the alpine zone of the Pyrenees above 2,500 m. (Bertrand, 1953). It is widely distributed in England, Wales and Ireland, but there is only one doubtful record for Scotland (Balfour-Browne, 1940). It frequents principally running water. I suggested (1952) from the examination of a few Yorkshire specimens that this was probably a flightless species, and specimens from southwest Germany showed the same evidence of incapacity for flight (1952, appendix). Since then I have received material from Rumney, Monmouthshire, (E.J.P.), from Frodsham Marsh, Cheshire, (H.B.N.H.), and from Basingstoke canal, Hants (F.D.G.). I have dissected both soft and mature specimens, and all confirm my previous view. Specimens which I collected recently in Denmark showed just the same modifications as the British *hyalinus*. The flightless characters of this species are in striking contrast to the condition found in *L. minutus* L., a species of about the same size or slightly smaller. In this, the flight muscles are usually very well developed, the wings are large (fig. 11) and the metatergum is strongly developed. The basalar and subalar discs of the pleural flight muscles are large and deeply sclerotic, but only the posterior one, the subalar is shown in the figure (fig. 11, Sa.).

The wings of *L. hyalinus* (fig. 12) are considerably smaller than those of *L. minutus* and much more frail, and the metatergum is almost transparent, shorter than that of *L. minutus*, and with the internal ridges feebly developed. The pleural discs are quite small. The flight muscles are either absent, or recognizable in some specimens

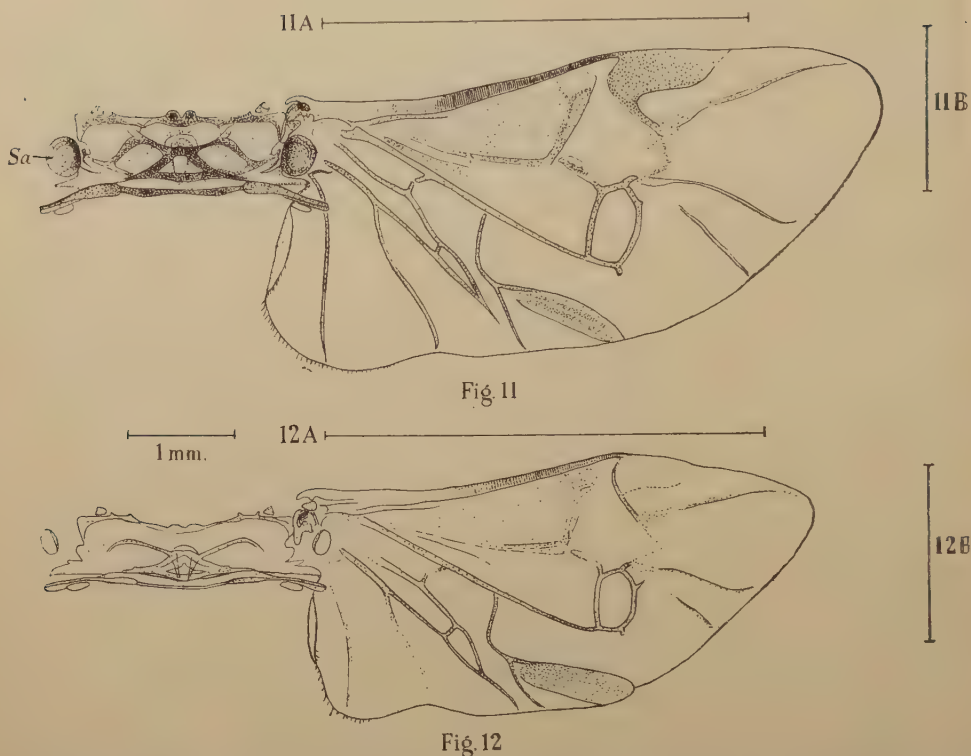


FIG. 11.—*Laccophilus minutus* L. Wing and metatergum, internal view, with subalar discs *in situ*, but rest of pleuron removed. From a mature male collected at Rumney, Monmouthshire, on 7th May, 1953, by the Rev. E. J. Pearce. Normal flight muscles, $\times 20\cdot8$. The length of the elytron at the same magnification is shown at 11, A and the width at 11, B.

FIG. 12.—*Laccophilus hyalinus* Deg. Wing and metatergum, internal view, with subalar discs *in situ*, but rest of pleuron removed. From a mature female collected in same locality on same day, by the Rev. E. J. Pearce. No flight muscles, $\times 20\cdot8$. The length of the elytron is shown at 12, A and the width at 12, B.

as thin fibres of abnormal histology. The muscles of the hind legs are enormously developed, not only for swimming, but in relation to the leaping powers possessed by the beetles of this genus.

I have seen *L. minutus* fly. It is rare in Fife, but specimens which I brought back from Hampshire in April were tested in a warm room at night. They soon commenced to leap about, covering several inches in one hop, and often landing on their backs, and then several flew in quick succession. Specimens from Lund, Sweden (C. H. L.) also had normal flight muscles.

In Africa, various species of *Laccophilus* have been captured at light (Guignot, 1953), and one, *L. quadrilineatus* Horn was similarly taken in America (Sherman, 1913). Needham & Williamson (1907) observed that another American species (presumably *maculosus* Germ.) can take to flight very quickly, suddenly emerging from trash floating on the surface of the water and springing into the air, using its wings as well as its legs, and then dropping back into the water.

Hygrotus quinque-lineatus Zett. compared with other *Hygrotus*.

This is a boreal species, widely distributed in Northern Europe. It should perhaps be included in the 'variable' class as one specimen has been taken in Fife with fairly well-developed flight muscles. I have dissected 20 other specimens, from Loch Garten, Inverness-shire, and from Lochs Fitty and Lindores in Fife. In these

the flight muscles were absent or abnormal, and though the beetles were tested for flight on several occasions, none attempted to fly. The restricted distribution of this species suggests incapacity for flight. In Fife, although it is known from two other lochs, I have only found it in the two lochs mentioned which both date from the close of the Glacial Period. In other districts its habitats are more varied (Balfour-Browne, 1940). Its metatergum and discs show nearly the same development as in *H. inaequalis* F., a common and widely distributed species, in which flying and flightless individuals occur. (Jackson, 1952). I have dissected a few specimens of *H. confluens* F., an 'English' species, which I took in a pool near York, and one from Herts (E.S.B.), and all have fully developed flight muscles: the metatergum is relatively longer than in *quinquelineatus* and darkly sclerotic, and the pleural discs are much larger.

Ilybius fenestratus F. compared with Flying *Ilybius*.

The Species Compared.

I. fenestratus F.

A species which usually exhibits flightless characteristics to a marked degree and has rather small wings. It is widely distributed abroad, occurring in northern and central Europe and in Siberia and North America (Horion, 1941), yet, in Great Britain it is a local species with a restricted range, and Balfour-Browne (1950) notes that it appears to be concentrated in certain spots. It is not recorded from Ireland. Size, as given by Fowler (1887), $11\frac{1}{2}$ by 6 mm.

I. subaeneus Er.

A species of the same size as *fenestratus*, widely distributed abroad and with a scattered distribution in Britain. A ready flier.

I. fuliginosus F.

A smaller species, 10 by 5 mm., common and widely distributed throughout the British Isles and occurring in North Africa, Europe, Siberia and North America. An excellent flier, always found with normal flight muscles, and often taken at light.

Ilybius fenestratus F.

Only rarely have I found specimens with normally developed flight muscles and in these the wings show the same reduction in size as in the beetles without flight muscles, and I have as yet no evidence that such individuals can fly. This species was recorded by Collett (1930) as being taken at light, but this record is erroneous. Dr. W. D. Hincks has kindly examined the specimen in Collett's collection in the Manchester University Museum and it is *I. fuliginosus*. It would be interesting to know if there are any authentic records of *fenestratus* flying and whether the specimen recorded by Walker (1906) as 'flying at Marston' was correctly identified.

The Material Examined.

I have dissected 21 British specimens, mostly from a brick pond at Acomb, Yorkshire, where I found the species very common in one small area on 3 July 1952. I think the species may have gregarious tendencies and if so inbreeding will occur, so that any mutations towards loss of flight will have every chance of being preserved. All the specimens dissected from here were flightless and the various tests for flight which I carried out were negative, and the beetles congregated in the shadiest part of the testing dish piled in a cluster, one on top of the other. Other flightless specimens came from Hants and Surrey (F.D.G.) and Bucks, and some without data but probably from Kirkcudbright (F.B.B.). Recently I have received three specimens from Yorkshire (T.B.K.). One was of the usual form without normal flight muscles, one had a partial development of flight muscles, and in the third specimen the flight muscles were fully developed. These specimens were tested for flight on the same evening as *I. subaeneus* from the same locality, but whereas the latter flew within a quarter of an hour, the *fenestratus* made no

attempt to fly, though watched for half an hour. When falling on their backs they whizzed round and round like a top but they never spread their elytra and wings to help them to get up, as *subaeneus* and *fuliginosus* were observed to do. I have dissected twenty-five specimens from Skane, Sweden, taken by Roth in 1878 (C.H.L.) and well preserved in alcohol. Most of them were flightless, but in four, normal flight muscles were present, but the wings of these specimens were no larger than in the others. (Table I and Pl. 1, fig. 16.) A few specimens which I collected in Denmark were of the usual form with abnormal flight muscles.

The Structural Modifications Observed.

In the genus *Ilybius* the cuticle of the metatergum and of the pleural discs is much paler and more transparent than in the genus *Agabus*, even in species with fully developed flight muscles. The prephragma and postphragma are transparent, so that the differences in the thorax between the flying and flightless species are not so striking as in *Agabus* with its more darkly sclerotic cuticle. In the common form of *I. fenestratus*, both mature and immature specimens were without normal flight muscles, in most, no flight muscles at all could be found, but in a few, very thin fibres of abnormal histology were present. In this form one finds the prephragma and postphragma undeveloped and the pleural discs small; in the rare form with normal flight muscles these parts were well developed and the flight muscles were of normal histology.

In all the specimens studied the wings are remarkably small for the size of the insect (Pl. 1, fig. 16), and very much smaller than in a species of the same size which flies (*I. subaeneus*, Pl. 1, fig. 17). On removing the elytra of *fenestratus* the folded wing, with its prominent intercubital plate, may be seen reaching only to the fifth or sixth tergite, rarely to the seventh, but in flying species such as *I. fuliginosus*, *I. ater* and *I. subaeneus*, the far more voluminous folded wings reach to the pygidium. In *fenestratus* the first abdominal spiracle is smaller than in *I. fuliginosus*. The abdomen of *fenestratus* is larger than a flying *Ilybius* being more convex dorsally, so that more space will be available for the reproductive organs, fat body and gut. *I. fenestratus* is characterized by very narrow metasternal 'wings', while in the 'flying' species mentioned the metasternal wings are wide. The narrow metasternal wings are correlated (as in *Agabus undulatus*), with a forwardly produced anterior coxal fold and a considerable increase in length of the flexor trochanter muscles compared with a flying species, and these modifications are the same in the rare forms with normal flight muscles. In these forms the pleural wing muscles are less parallel than in *fuliginosus* and the posterior branch of the *extensor alae posterior* is very short, as the space between the basalar disc and the anterior coxal fold is so narrow. Very noticeable in all *fenestratus* is the shortness of the metatergum as compared with that of species known to fly.

In the following table the length of the metatergum and the wing in *fenestratus* is compared with that of the other two *Ilybius*. I have included the width of the metatergum, measured from wing base to wing base across the anterior notal wing processes, as a guide to the size of the specimens, but in *subaeneus* though the two females were of full size, 11.5 mm., this measurement is less than in *I. fenestratus* of the same size, probably due to the greater curvature of the metatergum in the flying species.

It will be seen that while some variation exists in all three species in regard to the size of the wings, those of *fenestratus* may be considerably smaller even than the wings of the smaller *fuliginosus* (Pl. 1, fig. 15). Whether the *fenestratus* which have normal flight muscles are able to fly is questionable. In captivity the disappearance of these beetles from uncovered receptacles may be wrongly attributed to flight, for I have observed that they are able to climb up a nearly vertical wet surface and so make their escape.

The presence of normal flight muscles in insects incapable of flight is not unknown. Several examples are quoted by Poisson (1946) of the presence of muscles of flight

of normal appearance in insects in which the wings are atrophied. Thus Cuenot and Mercier (1923) record the persistence of vibratory muscles of flight in a mutant of *Drosophila melanogaster* Meig. with rudimentary wings, and Poisson (1923) observed that apterous individuals of *Limnotrechus thoracicus* Sch. and brachypterous *L. lacustris* L. had muscles of flight of normal appearance and striated, and the same was observed in five apterous examples of *Telia currens* Fab. a species which is mostly apterous.

TABLE I.

Table to show length of wing and metatergum in three species of *Ilybius*.

Species	Flight muscles	Width of metatergum	Length of metatergum	Length of wing from base of costa to tip of wing
<i>I. fuliginosus</i>		mm.	mm.	mm.
♂, Largoward, Fife	Normal	3.1	1.4	11.5
♀, St. Andrews, Fife	Normal	3.2	1.5	11.5
♀, St. Andrews, Fife	Normal	3.3	1.6	11.8
♂, Elgin (R. R.)	Normal	3.4	1.6	11.9
<i>I. fenestratus</i>				
♂, Acomb, Yorks.	None	4.0	1.3	10.9
♂, Acomb, Yorks.	None	4.4	1.2	10.6
♂, Yorks. (T. B. K.)	Abnormal	4.2	1.3	11.2
♂, Yorks. (T. B. K.)	Normal	4.1	1.3	10.8
♀, Skane, Sweden (C. H. L.)	Normal	3.6	1.1	9.9
♂, Skane, Sweden (C. H. L.)	Normal	4.1	1.3	10.8
<i>I. subaeneus</i>				
♀, Yorks. (T. B. K.)	Normal	3.9	1.6	12.7
♂, Yorks. (T. B. K.)	Normal	3.7	1.7	13.7
♀, Yorks. (T. B. K.)	Normal	3.9	1.7	13.0

DISCUSSION.

From the observations recorded above and from the data given in my previous paper (1952)* it is evident that great diversity exists in regard to the capacity for flight of water beetles. They range from excellent fliers to species in which the flight muscles are undeveloped, the metathorax modified, and the wings reduced in size. Such flightless species occur in many genera in the *Hydradephaga* and in some *Hydrophilidae*. A somewhat parallel case is shown by the aquatic Hemiptera in which flight reduction is exhibited in various degrees, and has been extensively studied by many entomologists, notably Poisson, Eklom and Larsén. Eklom (1941) observed that apterous *Gerris asper* L. survived hibernation better than macropterous individuals, and they were the first to appear on the water in spring. In *Coleoptera*, the work of Rüschkamp (1927) on loss of flight in Chrysomelids showed that some species with fully developed hind wings were yet incapable of flight, just as I observed in the weevil, *Sitona hispidulus* F. (1933). Larsén (1949) found that many macropterous Carabids showed more or less atrophied flying muscles, although the skeletal parts of the flying apparatus appeared to be well developed. He records an interesting case of asymmetrical development of the wings in a specimen of *Carabus clathratus* L., the wing of the right side being full-sized and that of the left side reduced, moreover, the left side of the metathorax showed smaller muscle discs and postnotum. A similar case of unilateral brachypterism is recorded by Leston (1952) in the bug, *Drymus brunneus* Sahlb.

* In addition to the brachypterous water beetles already mentioned (Jackson, 1952), three Dytiscids with rudimentary wings are recorded by Per Brinck (1948) from oceanic islands. These are *Bidessonotus* (*Liodesuss*) *involucer* Br. and *Senilius tristanicola* Br. from the islands of the Tristan da Cunha group, and *Anisomeria bistriata* Br. from Juan Fernandez.

Goldschmidt (1940), discussing wing reduction in insects, considers that the flying mechanism is reduced as a whole in consequence of a genetic change which affects development of the whole complex simultaneously. He does not believe that wing reduction in Carabid beetles necessitates the assumption of a gradual accumulation of micromutations, but can be explained by single steps, which change the relative rates of processes of growth and differentiation at an earlier or later time in development. He considers wing rudimentation in Coleoptera to be based on a single primary change in the growth differentiation of the wing discs. In the Dytiscidae we are concerned with certain species manifesting incapacity for flight in varying degrees, and one curious fact is that when the wings are partially reduced in size, they do not show a general all-over reduction, but rather a selective reduction, whereby the intercubital plate is preserved at almost its original size.

Sellier's work (1949 *a, b*) on the experimental production of macropterism in *Gryllus campestris* (a species normally brachypterous) suggests that brachypterism in the cricket results normally from a prolonged arrest of development at the 9th larval stage, in the course of which the wing rudiments lose a part of their power of growth. I found in breeding *Sitona* (1933) that there was a prevalence of forms without normal flight muscles amongst macropterous weevils emerging late in the autumn, and this may have been due to the delayed development. It is possible that in those species of water beetles in which the development of the flight muscles varies, environmental conditions during ontogenetic development may be a deciding factor, but where flight reduction involves brachypterism and correlated modifications of the metathorax, as in *Agabus undulatus* and *Noterus crassicornis*, a genetic factor is probably concerned. This was the case in the weevil *Sitona hispidulus* F. which exhibits wing dimorphism, and, in breeding experiments with this species, the proportion of macropterous to brachypterous offspring obtained from the various matings indicated that the brachypterous condition behaved as a simple Mendelian dominant (Jackson, 1928). I am at present studying a somewhat similar case of pronounced dimorphism of the flying apparatus in an African water beetle, *Agabus raffrayi* Sharp.

Many of the apparently flightless Dytiscidae in this country, though local here, have a very wide distribution abroad, and I already have some evidence which suggests that the development of the flying apparatus is usually much the same in continental specimens of the species I have examined, as in the British specimens. Such species probably became widely dispersed on the continent very long ago when more marshland existed than at present. Flightless species inhabiting fens and marshes have little opportunity of extending their range in a well cultivated country, and their present distribution must largely depend on the extent of swamps and boggy moorlands existing in the past, and on the survival of some such areas to the present day.

Loss of flight tends to restrict species to limited areas and may help to explain the peculiarly local distribution of certain species. There seems little doubt for instance that *Agabus undulatus* can only hold its own in relict areas of marsh and fen such as Askham Bog.

Flightless species frequenting running water will have greater chances of dispersal, and *Platambus maculatus*, which is widely distributed in Britain—though not known from the Isle of Wight or the Isle of Man or Ireland—probably reached Britain (with many other species) at the time of land connections with Europe, when British rivers were tributaries of continental rivers. Tate Regan (1911), in discussing the distribution of fresh-water fishes, states that such small species as the minnow or the loach, which thrive in little brooks, may be transferred from one river system to another by slight changes in the head waters. This would apply equally well to water beetles. Selection may well have favoured loss of flight in species adapted to life in running water, since flying individuals might not easily find other suitable waters. Species dwelling in lakes and boggy moorlands will have little occasion to fly. It is more difficult to understand what advantage loss of flight can be to a species such as *Agabus undulatus* which inhabits standing water, unless it has become

adapted to an environment of fens and marshlands now almost extinct. Moreover in all flightless beetles, the absence of flight muscles affords more space for fat body and the development of the reproductive organs, and these factors may be of selective value by increasing viability and fertility.

Wesenberg-Lund (1912) believes that various *Agabus*, *Colymbetes* and *Ilybius* spend a large part of their life out of water, and he comments on the amazing rapidity with which beetles of *A. guttatus*, in captivity, run over the ground. In damp areas, such as wet moorlands, it seems quite likely that flightless species will disperse in this way.

Some species which are good fliers are yet, apparently, restricted to the southern part of Britain, and it is probable that temperature is an important factor limiting their northward spread, as several of the 'English' species, though common on the continent, do not reach northern Europe. Not only may cold directly affect the beetle at some stage of its development, but a warm temperature appears to be essential to stimulate most species to flight, though others are known to fly even on mild days in winter. In Heteroptera, the effect of the higher average summer temperature on the continent on flying activity is noted by China (1930) who states that 'the British collector rarely sees his quarry flying, and, when visiting the continent, or even the Channel Islands, is surprised to see many species taking to flight at the slightest disturbance'.

More observations are required regarding the conditions which stimulate water beetles to fly. I have found that both sexually immature specimens and those with well developed reproductive organs have flown in tests, and even teneral specimens can fly. Popham (1952) has recorded the flight of *Acilius sulcatus* L. and *Gyrinus natator* L. from a drying up moorland pond in the end of September, but S. E. Allen informs me that he has found dozens of *A. bipustulatus* and *A. chalconatus* under stones in dried moorland pools. I have had a similar experience with *A. bipustulatus* both in June and October (1952).

Only further observations will make clear to what extent water beetles extend their range by flight, and much can be learnt if those taking water beetles in light traps will record their captures. I am inclined to think that comparatively few species are 'wanderers' and that the majority are dependant on a continuous stretch of ecologically suitable country for their gradual dispersal. Alpine and subalpine species have in all probability survived the Glacial Period in or near their present centres, and, as St. Claire Deville (1930) points out, their presence on British soil is likely to be ancient. These old inhabitants will persist in undisturbed areas of moorland and marsh, perhaps in very small numbers, and they may only occasionally be captured, so that caution is necessary before concluding that each new record for a district implies an extension of range.

SUMMARY.

The flight of various species of Hydradeephaga is recorded.

An account is given of the flight muscles and their skeletal supports in an *Agabus* capable of flight.

The reduction of the flight muscles and the modifications of the metathorax in *Agabus undulatus* are described. The first pair of abdominal spiracles, adjacent to the metatergum, is smaller than in a flying beetle of comparable size, and the anterior abdominal tergites are pale and membranous.

While the wings of *A. undulatus* are reduced in size, the dark intercubital plate, so characteristic a feature of the Dytiscid wing, shows no parallel reduction, and Heberdey's view of its function as one of the 'locking' devices of the elytra is discussed.

There is some evidence to suggest that in the genus *Agabus* species with narrow metasternal wings are flightless.

An account is given of flight reduction in *Agabus labiatus*, *A. uliginosus*, *Laccophilus hyalinus*, *Hygrotus quinquelineatus* and *Ilybius fenestratus*.

The possible bearing of these observations on the distribution of species is discussed, and the view is expressed that incapacity for flight may help to explain the local distribution of certain species frequenting standing water.

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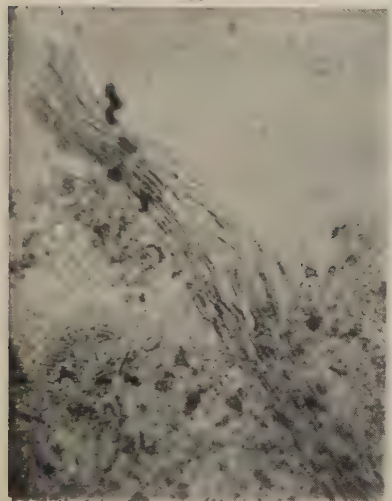
EXPLANATION OF LETTERING OF TEXT-FIGURES.

<i>A</i>	anal vein.	<i>D</i>	median notal process.
<i>ACF</i>	anterior coxal fold.	<i>EAA</i> , 1	extensor alae. anterior, anterior branch.
<i>AM</i>	abnormal flight muscle from basalar disc, amongst fat body.	<i>EAA</i> , 2	extensor alae anterior, posterior branch.
<i>ANP</i>	anterior notal wing process which articulates with the neck of the first axillary sclerite.	<i>EAP</i>	extensor alae posterior.
<i>AP</i>	apical plate of postnotum.	<i>Eps</i>	episternum.
<i>APh</i>	anterior phragma or prephragma.	<i>eps</i>	upper division of episternum
<i>AT</i> , 1	first abdominal tergite.	<i>FL</i>	furco-lateralis muscle, a tubular muscle going from the furca to the coxa at its junction with the episternum.
<i>Ax</i> , 1	first axillary sclerite, articulating on its outer side with the second axillary sclerite.	<i>FTL</i>	flexor trochanteris lateralis which arises from the highest part of the anterior coxal fold in <i>A. bipustulatus</i> .
<i>Ax</i> , 3	third axillary sclerite.	<i>FTM</i>	flexor trochanteris medius, arising from anterior coxal fold.
<i>AxC</i>	axillary cord.	<i>FTP</i>	flexor trochanteris posterior.
<i>BasMD</i>	basalar muscle disc.	<i>HC</i>	hind coxal fold.
<i>C</i>	costa.	<i>ICP</i>	intercoxal process.
<i>CD</i>	coxa-dorsalis muscle extending from median notal process to the spur of the hind coxal fold.	<i>IL</i>	internal lamina of coxa (Sharp D., 1882)
<i>CL</i>	coxal line.	<i>IP</i>	intercubital plate.
<i>CP</i>	coxal process.		
<i>Cum</i>	cuneus cell formed by anterior and posterior cubital veins.		

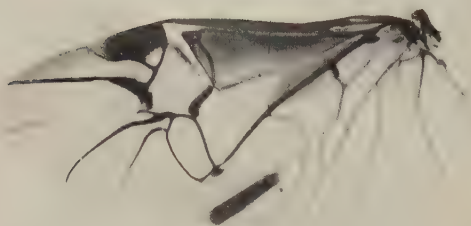
<i>IS</i>	oblique intrascutal ridge dividing the scutum into anterior and posterior parts.	<i>PNP</i>	posterior notal wing process which articulates with the lower portion of the third axillary sclerite.
<i>L</i>	line of attachment of first abdominal tergite, seen from beneath.	<i>PPh, 1</i>	area of postphragma to which the median metathoracic muscles are attached.
<i>LA</i>	<i>lateralis anterior</i> , a dorso-ventral indirect flight muscle.	<i>PPh, 2</i>	area of postphragma to which the lateral oblique muscles are attached.
<i>LE</i>	lateral edge of post-coxa, covered by epipleur of elytron.	<i>Prsc</i>	prescutum.
<i>LM</i>	<i>lateralis medius</i> , a dorso-ventral indirect flight muscle.	<i>R</i>	radius.
<i>LO</i>	lateral oblique muscle, an indirect flight muscle (<i>lateralis metathoracis posterior</i> of Bauer).	<i>RC</i>	radial or carpal cell.
<i>LPN</i>	lateral arm of postnotum.	<i>RE</i>	relaxator extensoris from basalar disc to edge of prescutum.
<i>M</i>	media.	<i>RR</i>	recurrent radius.
<i>MDP</i>	muscle disc on prescutum of <i>musculus relaxator alae</i> .	<i>Sa</i>	subalar muscle disc.
<i>MM</i>	median metathoracic indirect flight muscle.	<i>Sp</i>	spiracle of first abdominal segment.
<i>MS</i>	metasternum.	<i>Tr</i>	trochanter.
<i>MW</i>	metasternal "wing".	<i>V</i>	v-shaped ridge of scutellum.
<i>O</i>	oblongum cell.	<i>X</i>	cut edge of scutum.
<i>PC</i>	post-coxa, external lamina (Sharp D., 1882).	<i>Y</i>	apodeme from anterior edge of metasternum which forms the posterior part of the meso-coxal cavity.
<i>Pl</i>	cut edge of pleural membrane.	<i>Z</i>	prescutal process on which the suture of the elytron rests at its base.
<i>PN</i>	postnotum		



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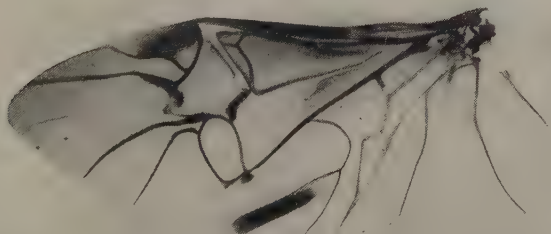
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FIG. 13.—*A. bipustulatus* L. A single fibre of normal indirect flight muscle, fixed Carnoy, stained Delafield's Haematoxylin, showing cross striation and nuclei. \times about 300.

FIG. 14.—*A. undulatus*. An entire abnormal flight muscle composed of many minute fibres with elongated nuclei, same magnification as Fig. 13.

FIG. 15.—*Ilybius fuliginosus* F. Wing of specimen from St. Andrews which flew. \times about $4\frac{1}{2}$.

FIG. 16.—*I. fenestratus* F. Wing of a specimen from Sweden, a larger beetle than *I. fuliginosus*, with normal flight muscles. Same magnification. (The elytron of *I. fenestratus* measured 9 mm. and that of *I. fuliginosus* only 8.5 mm.).

FIG. 17.—*I. subaeneus* Er. Wing of male with normal flight muscles, same magnification.

A NOTE ON THE BIOLOGY OF BRECHITES PENIS (L.) (LAMELLI-BRANCHIA). By R. DENISON PURCHON, Ph.D., Raffles Professor of Zoology, University of Malaya, Singapore.

(With 8 text-figures.)

[Read 21 April 1955.]

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INTRODUCTION.

While collecting on the sea shore at Bedok on the South East coast of the island of Singapore on 4 March 1954, a single living specimen of *Brechites penis* (L.) was found lying on the surface of muddy sand at low water mark of spring tides. The opportunity was taken to learn as much as possible of the ciliary feeding and cleansing mechanisms of the animal, and the fragments of the shell were sent to Dr. R. Tucker Abbott, at the Smithsonian Institution, Washington, for identification. The specimen was identified as *Brechites penis* (L.), with which *B. javanus* Bruguière was considered to be synonymous. The writer wishes to express his sincere thanks to Dr. Tucker Abbott for his expert help.

Lamy (1923), referring to *V. vaginifer* Lamarck, stated that the genus had been named *Penicillus* by Bruguière in 1792, and *Aspergillum* by Lamarck in 1818, but that these were antedated by the name *Brechites* Guettard, 1770. Winckworth (1945) observed that Guettard's nomenclature was not binomial and therefore was invalid. Dr. Tucker Abbott advised the writer (in a personal communication) that it would be best for the present, however, to continue to follow Thiele (1934) and use the generic name *Brechites*.

Brechites is placed with one other genus, *Clavagella*, in the little-known family Clavagellidae. In both *Clavagella* and *Brechites* the animal lies within a tubular adventitious shell. In *Clavagella* the left shell valve is fused with the inner surface of the shelly tube, whilst in *Brechites* both shell valves actually form a small part of the tube antero-dorsally, and have lost the ability to articulate upon one another at the original hinge line.

Pelseneer (1906) placed the Clavagellidae in the suborder Anatinacea, as did Ridewood (1903). Thiele (1934), on the other hand, placed the Clavagellidae by itself in the stirps Clavagellacea in the suborder Anomalodesmata. There are very few references to the Clavagellidae in literature, and the majority of these are concerned with the shell of recent or of fossil forms (e.g. Tate, 1886; Sowerby, 1888).

With regard to *Brechites*, the only anatomical studies appear to be those of Lacaze Duthiers (1870, 1883). The paucity of literature is compensated by the excellence of the last-mentioned paper, and the writer is deeply indebted to Professor C. M. Yonge, F.R.S., who kindly placed his personal copy of this paper at the writer's disposal.

Lacaze Duthiers (1883) listed five 'species' of *Aspergillum* (= *Brechites*), three of which came from Singapore, and one from Java. He had the animal as well as the shell in only two of these. Fragments of the shell of *Brechites* sp. have been obtained at rare intervals locally, both inter-tidally and in dredge hauls offshore from a muddy bottom. An intact locally collected shell of *Brechites* (labelled *Verpa annulosa* Deshayes, and probably synonymous with *B. penis* (L.) is displayed in the Raffles Museum, Singapore. It is probable, therefore, that *Brechites* is not uncommon in Singapore waters, but, having found only one living specimen in four years of sporadic field work, I think it improbable that further living specimens will be found in the near future. This paper is therefore presented as the study of a single living specimen.

THE SHELL.

The shell of the specimen studied was unusual in that towards the posterior end there was a right angle bend, the terminal 3.5 cm. of tube being directed dorsally (Fig. 1). It was concluded that the shell was probably originally buried vertically in the substratum, perhaps offshore, but had been washed out and had thereafter lain horizontally on the surface of the mud. This may have led to the formation of an extension at right angles to the long axis of the shell, to carry the orifices of the siphonal process clear of the substratum to a point where clean sea water could be obtained.



* FIG. 1.—*Brechites penis*. Shell, seen from the left side. Magnification $\times 2/3$.

Lacaze Duthiers (1883) distinguished between a 'true shell' and a 'false shell'. The 'true shell' (fig. 1, TS) may be taken to represent the original shell valves, both of which are incorporated in the wall of the tube, and which may be recognized externally by the two umbones and by a series of concentric growth lines ventral to the umbones. On the inner surface of the tube the 'true shell' is distinguished by the pallial line (fig. 2, PL) where the pallial muscles are inserted into the shell, and by the line along which the sheath of periostracum is inserted into the shell (Fig. 2, AP, VP, PP). In the region of the 'true shell' the mantle tissues lie in direct contact with the shell, and there are muscle attachments, whereas the remainder of the animal is covered with a delicate periostracal sheath that lies between it and the 'false shell' (fig. 1, FS). Lacaze Duthiers considered from this evidence that there are probably two phases in the life of the animal, one in which the two shell valves are growing by peripheral increments and in which they probably articulate upon one another at the hinge line, and a second phase in which an adventitious shell tube is formed, into which the 'true shell valves' are incorporated, and after the onset of which there is no further growth in the diameter of the tube. Lacaze Duthiers compared the structure of the 'false shell' and of the periostracum, and showed that there were important features in common, in the presence of calcareous crystals on the interior of the 'false shell' and on the exterior of the periostracum.

* See pp. 53-4 for Key to the Lettering on the Figures.

Lacaze Duthiers noted two apertures on the surface of the tube. One of these was in the centre of the perforated anterior disc (Fig. 1, D), and corresponded with the position of the pedal aperture in the mantle and periostracum within: a slit-shaped aperture in such a position was noted in the present study. The second aperture noted by Lacaze Duthiers lay mid-ventrally, between the lower borders of the 'true shell', and corresponded with the position of a fourth pallial

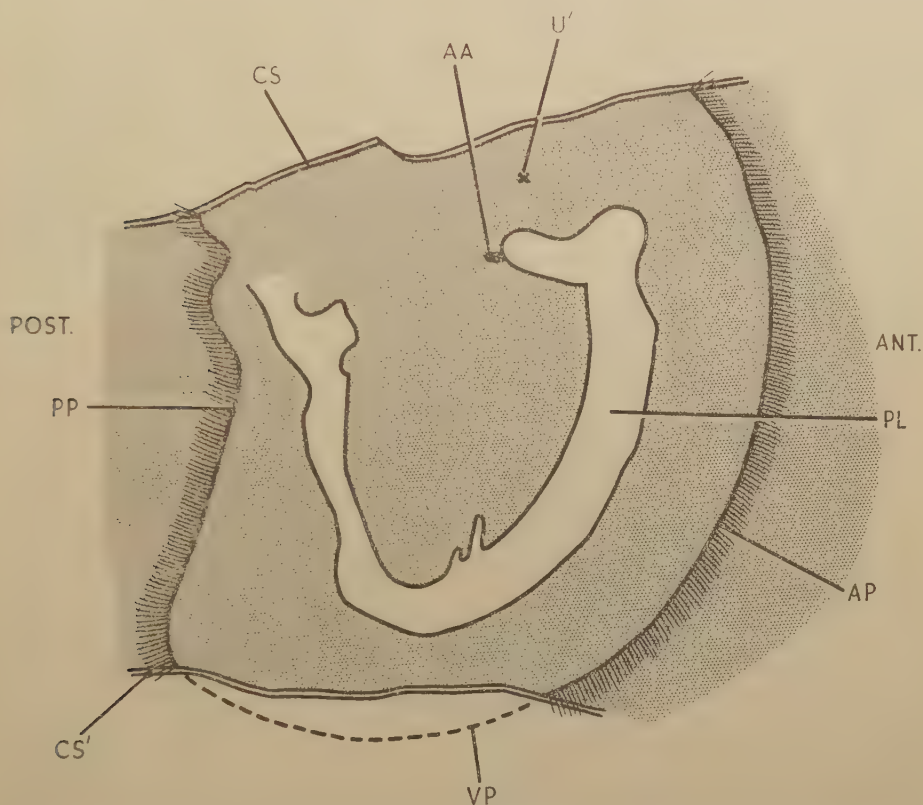


FIG. 2.—*Brechites penis*. View of the interior of the anterior end of the tube, showing the left 'true shell'. Magnification $\times 5.4$.

aperture which he noted within. Lacaze Duthiers stated that this mid-ventral aperture might degenerate, and the fact that no such aperture was seen here may be taken in support of this view.

THE SIPHONS.

The siphons are fused to the very tips (fig. 3, EX, IN), and are covered to the tip by a thin, tough, but transparent sheath of periostracum (fig. 3, P). The siphons are therefore of type 'C' as described by Yonge (1948). The presence of an adventitious tube of 'false shell' around the siphonal process is an unusual feature, but this tubular posterior extension of the shell differs from that described for the Cuspidariidae by Yonge (1948) in being separated from the flesh of the siphonal process by a continuous sheath of periostracum.

At the base of the siphonal process the periostracal sheath is inserted into the inner surface of the tube dorsally and laterally (fig. 2, PP). Ventrally the periostracum passes forwards as a thin strip, and the sides of this strip of periostracum

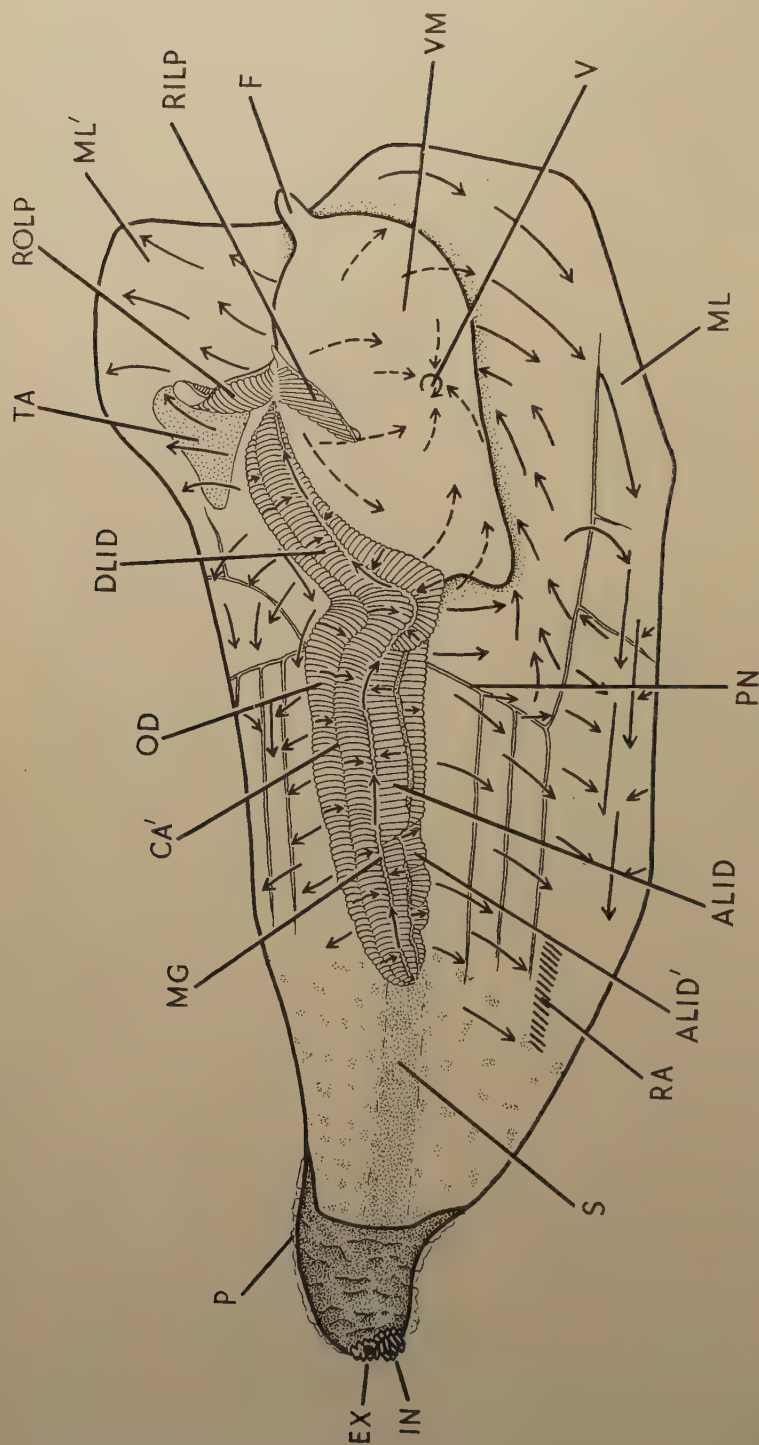


FIG. 3.—*Brechites penis*. Contents of the mantle cavity. A horizontal lateral incision has been made in the right wall of the mantle, and the flaps of mantle have been pinned down. The broken arrows in the region of the visceral mass indicate the course of the ciliary currents on the inner surface of the mantle in this part of the body. (The ciliary currents on the surface of the visceral mass are shown in fig. 7.) Magnification $\times 3.3$.

are inserted into the inner side of the tube (fig. 2, VP) along the lower border of the 'true shell'. Anterior to the true shell, the periostracum expands into a transverse sheet which lies between the anterior end of the animal and the perforated disc (fig. 1, D) closing the anterior end of the tube. In the centre of this anterior sheet of periostracum there is a small aperture at the margin of which the periostracum joins the rim of a small pedal orifice in the mantle, which is otherwise wholly fused. Laterally, the margins of this anterior transverse sheet of periostracum are inserted into the inner side of the tube (fig. 2, AP) along a line forming the anterior margin of the 'true shell'.

Lacaze Duthiers observed a 'fourth' aperture in the mantle, mid-ventrally opposite the 'true shell', and a corresponding aperture in the periostracal sheath. In the present study no such fourth aperture was seen, though the animal was studied alive, and the mantle cavity was opened by a longitudinal lateral incision that would not have damaged such an aperture, had it been present. As stated by Lacaze Duthiers, this fourth pallial aperture, and the corresponding aperture in the shell outside, may become degenerate, and disappear.

The inhalent aperture is wider than the exhalent aperture, and has about 12 long simple tentacles that tend to arch over the aperture. External to these are more numerous, smaller simple tentacles and outside these, a ring of very small papillae. The exhalent aperture is bordered by a delicate membrane that can be introverted. The tentacles and the terminal part of the siphonal process are black, the pigment being laid down in close transverse lines. Anteriorly, the pigment is reduced to scattered groups of pigment spots, which are accompanied by scattered groups of pale yellowish brown dots: there are also deep-lying opaque white masses. The walls of the siphonal process are thick, and when cut they exude a white opaque substance, as is the case also in the Teredinidae.

MUSCULATURE.

When the animal was fully relaxed, the tip of the siphonal process was just seen at the posterior aperture of the shell (fig. 1, PO) the animal being about 16 cm. in length when fully expanded. When the shell was opened, the siphonal process gradually withdrew, contraction being effected wholly by distributed muscular contractions, and not by introversion of the base of the siphonal process. When fully exposed, the whole animal measured approximately 5.5 cm., about one-third of its maximum length.

Examination of the pallial line (fig. 2, PL) shows that there is no pallial sinus, which is unusual for a bivalve with such a long and highly contractile siphonal process. At the same time it will be noted that the scar produced by the insertion of the pallial muscles on the interior of the tube is very broad, indicating the great development of the pallial muscles. A comparison may be drawn with the Teredinidae where, however, the posterior end of the siphonal process is firmly attached to the interior of the shell-lined burrow, and where accordingly the siphonal process (or posterior extension of the mantle cavity?) cannot be extensively withdrawn.

Lacaze Duthiers was unable to find any trace whatsoever of a posterior adductor muscle, and stated that, due to its loss, the visceral ganglia occupied an unusual position, directly below the rectum. He sought the anterior adductor muscle and considered that, if it were present, it must be atypical. In the present study, four small but distinct muscle bundles were found crossing the body transversely, dorsal to the oesophagus. The adductor scar itself could not be distinguished on the interior of the tube, but its approximate position and size are indicated in fig. 2 (AA). The absence of a posterior adductor is confirmed.

Haas (1929-41), who relied on the descriptions of Lacaze Duthiers, considered *Brechites* to be a monomyarian comparable with other forms such as *Tridacna*, *Mulleria*, Limidae, Ostreidae, Pectinidae, etc. It is now clear, however, that *Brechites*, if not the Clavagellidae as a whole, is unique as a monomyarian in having lost the posterior adductor, and not the anterior adductor. It is also unusual in

that the remaining adductor muscle is itself greatly reduced in size, not augmented. This is due to the complete loss of articulation of the shell valves, and it is perhaps only a matter of chance that in the course of reduction of the adductor muscles, some trace yet remains of the anterior adductor muscle in the adult animal. A reason for this, however, may be found in the early phase of the life history of the animal. From a functional standpoint, it would be better to disregard the minute anterior adductor of the adult animal, and define the adult as 'anyarian'.

There is no trace of either the anterior or the posterior retractor muscles of the visceral mass. There are no transverse muscle fibres running through the visceral mass, nor are there even any superficial muscle fibres associated with the membrane covering the surface of the visceral mass. This degeneration of the muscular system must be without parallel in the Lamellibranchia.

THE MANTLE CAVITY.

The mantle cavity was opened by a horizontal lateral incision in the right mantle wall, and the mantle flaps so produced were deflected upwards, and downwards, and pinned out. The disposition of the organs in the mantle cavity is best understood by reference to fig. 3, and a detailed description is unnecessary.

a. *The Ctenidia.* Lacaze Duthiers described the ctenidium as consisting of a complete inner demibranch with descending lamella (figs. 3, 4 and 5. DLID) and ascending lamella (ALID) and of an outer demibranch consisting of a direct lamella only (OD). Posterior to the visceral mass the upper margins of the ascending lamellae of the two inner demibranchs meet and fuse in the middle line (fig. 4. FC). His findings are confirmed in this study. Lacaze Duthiers figured a ctenidial axis running longitudinally between the outer and inner demibranchs. In the present

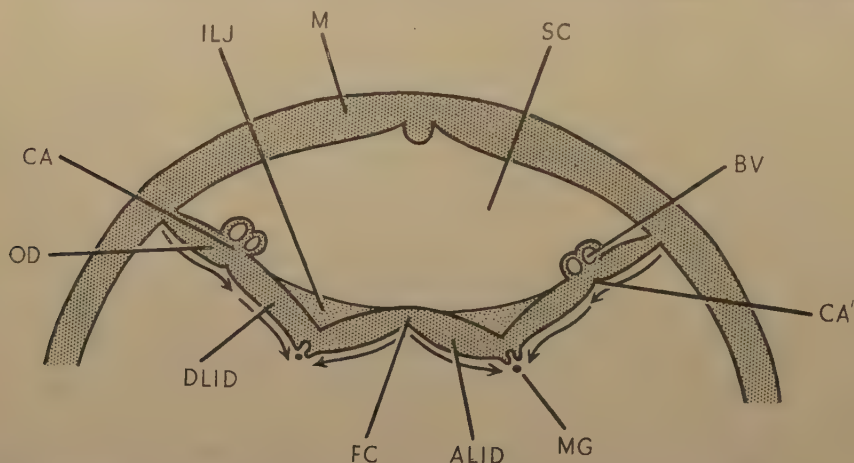


FIG. 4.—*Brechites penis*. Diagrammatic transverse section through the dorsal part of the mantle cavity, posterior to the visceral mass, to indicate the structure of, and ciliary currents on the ctenidia. Magnification $\times 10$, approx.

case, on the other hand, no such longitudinal structure was to be seen and it was only by close scrutiny that a distinction was drawn between the outer demibranch (OD) and the descending lamella of the inner demibranch (DLID). The reason for this was that in the specimen studied there was a fusion between each plica of the outer demibranch and the corresponding plica of the descending lamella of the inner demibranch, thus completely obscuring the ctenidial axis. It is improbable that Lacaze Duthiers could have worked on a specimen exactly comparable to that studied here. What is more probable is that there is a difference of this order between two species of *Brechites*, and that the two accounts are based on different species, or that there is a variation of this order within one species.

Ridewood (1903) stated that the ctenidia of *Brechites* are plicate and heterorhabdic, there being an average of 20 filaments per plica in *B. javanicus*. He stated that the ctenidial structure of *Brechites* is uniform throughout the Anatinacea including the Clavagellidae, Anatinidae, Pandoridae, Lyonsiidae, and probably also the Chamostreidae. This ctenidial structure is defined as type 'E' by Atkins (1937 a), and occurs in the Anatinacea, and also in the Tellinidae and Semelidae. Atkins (1937) stated that in species studied in the Anatinacea the principal filaments of the up-turned outer demibranch are continuous with those of the descending lamella of the inner demibranch, and the plicae of the one with those of the other. There is no interruption of the passage of particles across the axis. This is true also of *Brechites*.

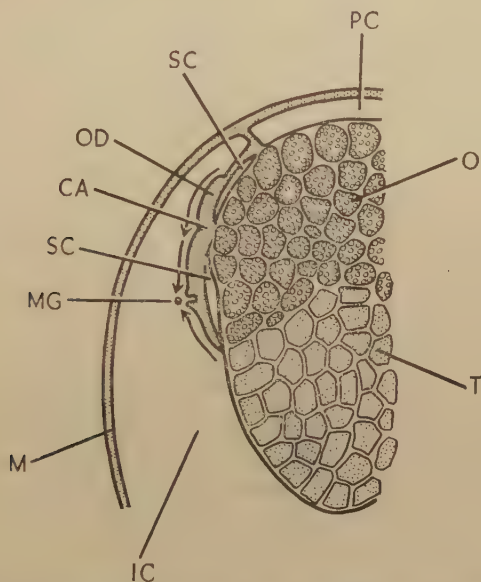


FIG. 5.—*Brechites penis*. Diagrammatic transverse section through the body in the region of the pericardium to indicate the structure of, and ciliary currents on the ctenidia. Magnification $\times 5$.

On all parts of the ctenidia, both on the crests of the plicae and in the troughs between the plicae, cilia beat towards the marginal groove running along the ventral margin of the inner demibranch. As indicated (figs. 3, 4 & 5), particles travelling ventralwards over the surface of the outer demibranch are carried across the region of the ctenidial axis, and on to the descending lamella of the inner demibranch.

At the point of fusion between any one plica of the outer demibranch and the corresponding plica of the inner demibranch, there is an inconspicuous notch. There is a vertical mark on both anterior and posterior sides of the fused plicae at this point. The particles being carried ventralwards on the filaments of the outer demibranch may not be transferred directly to a corresponding level on the plica on the other side of the point of fusion, but commonly pass downwards to the base of the trough at the point of fusion, and then turn upwards again on the far side of the fusion, regaining a position high on the side of the plica. This detail of ciliary action proves beyond doubt that the present structure of the ctenidium has been derived by fusion of plicae across the ctenidial axis.

Detailed examination of the marginal groove shows that the plicae do not flatten out here, as in *Tridacna* (Purchon, 1955 a) but form a scalloped margin to the groove (fig. 6). The marginal groove can be widely opened, when all material carried towards the groove on the crests of the plicae, or in the troughs, is passed into the groove.

The marginal groove may be closed, on the other hand, and then only the particles travelling in the plical grooves are able to enter the depths of the marginal groove, to be transported oralwards to the mouth. Material travelling on the crest of a plica is unable to pass deep into the marginal groove, and is ultimately rejected from the ctenidium. The nature of this sorting mechanism is illustrated (fig. 6). Atkins (1937) stated that Lamellibranchia with this form of ciliary sorting mechanism include *Pinna fragilis* Pennant, *Cochlodoma praetense* (Montagu), *Lyonsia norvegica* (Gmelin), *Thracia villosiuscula* (Macgillivray) and *Thracia distorta* (Montagu).

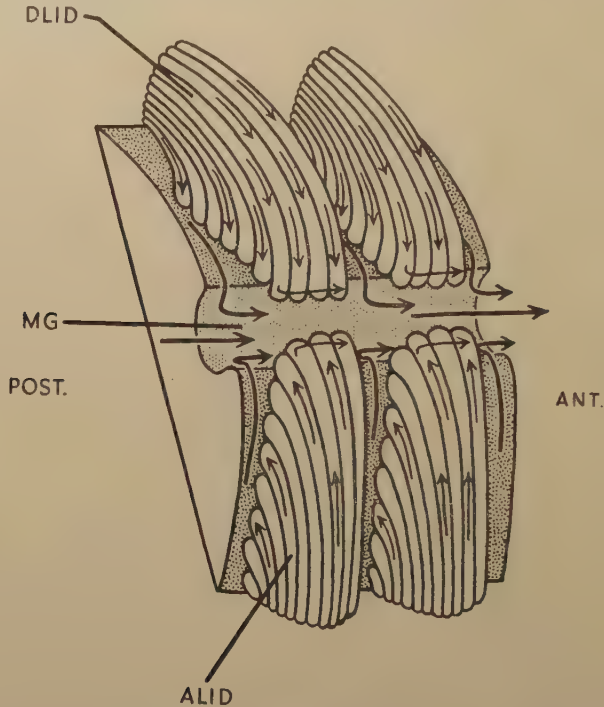


FIG. 6.—*Brechites penis*. Diagrammatic representation of a part of the marginal groove of the right inner demibranch, showing the plicate structure of the ctenidium, and the mechanism whereby particles travelling in the bottoms of the plical troughs are admitted into the marginal groove. Magnification undetermined.

The marginal groove of the inner demibranch discharges posterior to the bases of the labial palps on to the smooth area that lies between the bases of the labial palps. Material from the marginal groove of the ctenidium passes into this proximal oral groove without having been subjected to selective action by the labial palps.

b. The Labial Palps. The palps are of moderate size, with well developed inner folded surfaces (figs. 3 & 7, ROLP, RILP). The lips of the mouth are deep, and the anterior lip has a delicate rim which overlaps the posterior lip, thus making the proximal oral groove virtually a closed tube.

The labial palps are not very effective as organs of selection and rejection. If a considerable quantity of fine carborundum—of Grade F 3—is pipetted on to the folded surface of the palps, the predominant movement is oralwards over the crests of the folds. A lesser amount of carborundum passes dorsalwards along the distal sides of the folds, and relatively little passes into the depths of the grooves to be conveyed ventralwards to the free ventral margin of the palp.

Particles that pass oralwards over the most anterior fold, come to lie in a groove anterior to this fold. In this groove, the material is collected into a mucus-bound cord which rotates on its axis. The rotation is downwards on its posterior side, and upwards on its anterior side. Sometimes small particles become detached on the anterior side of the cord, and pass forwards and into the proximal oral groove. The cord itself slowly moves ventralwards and passes on to the free ventral margin of the palp, where it is conveyed backwards and ultimately is transferred to the mantle.



FIG. 7.—*Brechites penis*. Ciliary currents on the right side of the visceral mass and the foot. Magnification $\times 5.4$.

The details of the ciliary pattern on the folded surfaces of the palps are as follows.

1. An oralward current over the crests of the folds, and down the upper half of the proximal slope of the folds.
2. Ventralwards, towards the free ventral margin of the palp, on the lower half of the proximal slope, and on the floor of the grooves between the folds.
3. Oralwards, up the lower half of the distal slopes of the folds.
4. Dorsalwards towards the base of the palp, half way up the distal slopes of the folds.
5. An aboral rejection current along the free ventral edge of the palp.

The above details are illustrated in diagrammatic form (fig. 8). It will be noted that there is a transverse shelf half way down the anterior side of each fold. When the folds are in their normal position, each partly overlapping the fold in front of it, this shelf partly covers the depths of the groove and hinders the passage of particles into the rejection currents in the depths of the grooves.

It has been stated above that the labial palps of *Brechites penis* are very weakly developed as selective and rejecting organs. This is primarily due to the absence of a ventralward re-sorting current on the folds. In some lamellibranchs such a current occurs on the anterior sides of the folds, and exercises a powerful influence in rejecting material from the folded surfaces of the palps, e.g. in the Pholadidae (Purchon, 1955). *Brechites penis* probably lives buried in a soft substratum on sheltered coasts, either in the vicinity of low water mark, or sub-littorally. Under such circumstances the water should ordinarily be calm, and there should be little turbidity. If this is true, then the weak selective action of the labial palps is an adaptation suitable to the habitat and mode of life of the animal.

c. *The Visceral Mass.* The visceral mass is a soft, rounded, structure the upper half of which is largely composed of an ovary, yellowish brown in colour. The lower half of the visceral mass is occupied by the pure white lobes of the testis, and the line of demarcation between ovary and testis is very clear (fig. 7, O, T). Anteriorly there is a small and inactive foot (F). Owing to the absence of any retractor muscles of the visceral mass, and the absence of muscle fibres running through its substance, the visceral mass is soft and inactive.

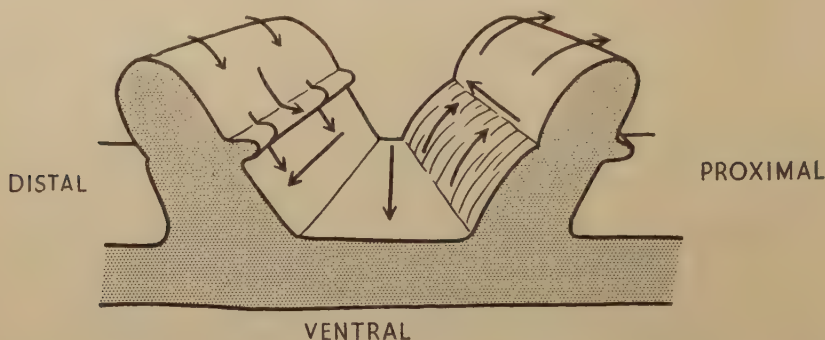


FIG. 8.—*Brechites penis*. Diagrammatic representation of a portion of the inner surface of the right inner labial palp to show the details of ciliary action.

Ciliary cleansing currents on the surface of the visceral mass are predominantly downwards and backwards, as is shown (fig. 7). A particularly strong current sweeps down from the region of the inner labial palp (RILP) and joins another current running backwards along the middle of the side of the visceral mass.

The skin of the visceral mass is thin and transparent, but is tough. It contains no muscle fibres.

d. *The Mantle.* The ciliary cleansing currents on the inner surface of the mantle are depicted (fig. 3). Broken arrows are used in this figure to indicate the course of ciliary currents on the area of mantle that lies hidden by the visceral mass.

In the posterior part of the mantle cavity, behind the visceral mass, the general trend of ciliary activity is downwards and backwards, there being a powerful rejection tract in the mid-ventral line which carries waste material backwards to the base of the inhalent siphon. Minor damage by the insertion of pins into the mantle may be the reason for the presence of a small area where particles tended to collect postero-ventrally (fig. 3, RA).

Anteriorly, opposite the visceral mass, ciliary currents passed from all directions towards a vortex (fig. 3, V) where particles circulated in a clockwise direction on the left mantle lobe. This vortex would seem to be out of reach of the labial palps, and its significance is not clear. In all probability any material collecting here would be transported backwards from time to time by the strong posteriorward cleansing currents on the sides of the visceral mass.

SUMMARY.

1. A single living specimen of *Brechites penis* (L.) was obtained at low water mark on a sheltered beach on Singapore island in March 1954.
2. With the exception of a small area near the anterior end, where the pallial muscles are inserted into the shell, the remainder of the animal is separated from the calcareous tube by a continuous sheath of periostracum.
3. The posterior adductor muscle is absent, and the anterior adductor is reduced to four small muscle bundles. This condition is described as 'amyarian'. There

are no retractor muscles of the visceral mass, nor does the surface of the visceral mass contain any muscle fibres. The pallial, and siphonal muscles are highly developed.

4. The ciliary sorting and cleansing mechanisms on the ctenidia, labial palps, visceral mass and mantle are figured and described.

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KEY TO THE LETTERING ON THE FIGURES.

AA	Probable position and size of the anterior adductor scar.
ALID	Ascending lamella of the right inner demibranch.
ALID'	Ascending lamella of the left inner demibranch.
ANT	Anterior.
AP	Anterior line of insertion of the periostracum on to the inner side of the shell.
BV	Blood vessels in the ctenidial axis.
CA	Ctenidial axis.
CA'	Fusion of demibranchs over the ctenidial axis.
CS	Cut surface of shell, dorsal.
CS'	Cut surface of shell, ventral.
D	Disc of shell.
DLID	Descending lamella of the inner demibranch.
EX	Exhalant siphon.
F	Foot.
FC	Fusion of left and right inner demibranchs.
FS	False shell.
IC	Infra-branchial chamber.
ILJ	Inter-lamellar junction.
IN	Inhalant aperture.
LAID	Line of attachment of the inner demibranch.
M	Mantle
MG	Marginal groove of the inner demibranch, with an oralward food current.
ML	Left mantle lobe.

<i>ML'</i>	Right lobe of the mantle.
<i>O</i>	Ovary.
<i>OD</i>	Outer demibranch
<i>P</i>	Periostracum
<i>PC</i>	Pericardium
<i>PL</i>	Pallial line
<i>PN</i>	Pallial nerve
<i>PO</i>	Posterior orifice of shell.
<i>POST</i>	Posterior.
<i>PP</i>	Posterior line of insertion of the periostracum on to the inner side of the shell.
<i>RA</i>	Region where particles tend to accumulate.
<i>RILP</i>	Right inner labial palp.
<i>ROLP</i>	Right outer labial palp.
<i>S</i>	Septum in the siphonal process separating the inhalent and exhalent canals.
<i>SC</i>	Supra-branchial chamber.
<i>T</i>	Testis.
<i>TA</i>	Transparent area in the mantle.
<i>TS</i>	True shell.
<i>U</i>	Umbonal region of the true shell.
<i>U'</i>	Umbonal region, seen ventrally.
<i>V</i>	Vortex in the ciliary sorting mechanisms.
<i>VM</i>	Visceral mass.
<i>VP</i>	Probable line of attachment of the periostracum ventrally.

THE STRUCTURE AND BIOLOGY OF VALLICULA MULTIFORMIS, GEN.
ET SP. NOV., A PLATYCTENID CTENOPHORE. By J. J. RANKIN, B.Sc.,
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F.R.S., F.L.S.)

(With Plates 2-3, 8 text-figures and 1 table.)

[Read 21 April, 1955.]

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INTRODUCTION.

Upon examination of the recently discovered Jamaican Ctenophore mentioned in a preliminary notice (Rankin, 1951) it has been found that in many respects it differs from the other genera of Platyctenida and that it shows several new characters such as oral lappets and marked oral grooves. It has therefore been necessary to create an entirely new genus of the order Platyctenida for the reception of this form.

On this basis the Platyctenida includes seven genera, namely, the creeping *Coeloplana* Kowalevsky (1880), the pelagic *Ctenoplana* Korotneff (1886) and *Planoctena* Dawydoff (1936), the parasitic *Gastra* (= *Gastrodes* Korotneff, 1888), the sessile *Tjalfiella* Mortensen (1910) and *Lyrocteis* Komai (1942), and the genus which I propose to call *Vallacula* which has diversity of habit, being sometimes creeping, sometimes floating in the plankton and sometimes sessile on hydroids or ascidians. *Vallacula* can also be shown to be intermediate in structure between *Coeloplana* and *Lyrocteis*, thus providing a further stage in the morphological series from the planktonic *Ctenoplana* to the completely sessile *Tjalfiella*.

MATERIAL.

The present description is based on a holotype (No. 3277) and six paratypes (No. 3278) in the American Museum of Natural History and on paratypes in the author's collection in the Zoology Museum, University College of the West Indies. The holotype is preserved in 'cellosolve' (ethylene glycol monoethyl ether) and the paratypes are either similarly preserved in various characteristic attitudes or stained and mounted as microscopical preparations.

METHODS.

The holotype and all paratypes were studied first in the living state in their natural surroundings, then removed to aquaria and finally observed and photographed under phase contrast microscopy. All specimens were killed and fixed by the carbon dioxide freezing method especially devised for them (Rankin, 1953) and either preserved in 'cellosolve', which has the advantage of rendering the canal system visible, or prepared for microscopical work.

HABITAT.

The first specimens (Rankin, 1951) were found in the mangroves of the Palisadoes of Kingston Harbour, Jamaica, in the region where there is a narrow 'cut-through' connecting the harbour with the lagoons leading into the open sea. The water in this vicinity therefore flows somewhat sluggishly and its salinity depends on the degree of man-made clearance of mangroves from the 'cut-through', and also on the rainfall. *Vallicula* occurs in largest numbers generally from June to September and January to March, and is found in sparse numbers during the rains of May, October and early December. Generally it is found together with *Synaptula hydriformis*, the viviparous holothurian, clinging to hydroids of the dynamenid group and to algae such as *Acanthophora spicifera* and *Caulerpa sertularioides* (Gmel.) Howe, forma longisetata. Specimens found in this habitat generally tend to be pinkish or greenish in colour when found, but may become paler if removed to an aquarium without algae. *Vallicula* may also be found crawling over the blue-black tests of *Ascidia nigra* Savigny, and it then tends to be completely colourless or only lightly pigmented in the apical and tentacular regions. Specimens have also been found at the harbour entrance crawling over ascidians attached to jetties and a few have been found on ascidians in a neighbouring 'cut-through' and in nearby lagoons. Other specimens have been taken in surface tow-nettings off the shore at Port Royal.

MACROSCOPICAL ANATOMY.

Size.

The holotype is one centimetre in length along the tentacular axis and paratypes range in size from one millimetre to thirteen millimetres, including some immature forms. The largest forms are fully mature but forms under five millimetres tend to be juvenile in appearance, i.e. with the various parts of the tentacle sheaths and canal system not clearly differentiated. The tentacle length also increases relative to the body size until in immature specimens the tentacles when fully extended may be from twenty to thirty times the length of the body.

Colour.

The pigment varies in colour, three types being superficially recognizable. Almost all specimens examined possess a brown pigment located in cells which resemble chromatophores and which can readily be seen in surface view (Pls. 2D, 3A, 3B). They are densely concentrated in the region of the apical organ and tentacle sheaths, and are scattered more diffusely around the periphery. In transmitted light these cells have a brown appearance but in reflected light they appear whitish and somewhat suggestive of air cells.

Occasionally pale green cells are also seen and when present (generally in specimens which have been resting on the green alga *Caulerpa sertularioides*) they are scattered over the entire aboral surface and clearly distinguishable from the brown cells. Small red globules are present in most forms and tend to be found near the brown pigment cells. When present in large numbers they give a pinkish hue to the animal.

Shape.

Vallicula is capable of assuming various forms, at least four of which are clearly distinguishable and may be termed (a) gliding, (b) creeping, (c) floating, and (d) sessile phases. The animal is capable of passing rapidly from one phase to another. See fig. 1.

(a) *Gliding phase.*

In this form the animal is completely flattened in the oral-aboral plane, bearing a general resemblance to *Coeloplana*, and is capable of gliding over the substrate or under the surface film by means of the numerous cilia on the whole of the oral surface. The peripheral rim of the animal is perpetually, although not rhythmically, moving. The typical body form when in the gliding phase may be seen in Pl. 3A, and text-fig. 1A. Here the oral groove is very shallow and sometimes a little difficult to see and the 'mouth' is closed. The aboral papillae may also be partially if not wholly withdrawn.

(b) *Creeping phase.*

This is very similar to the gliding form but is not so flattened. The edges of the oral grooves are pronounced and near the mouth are produced into lappets

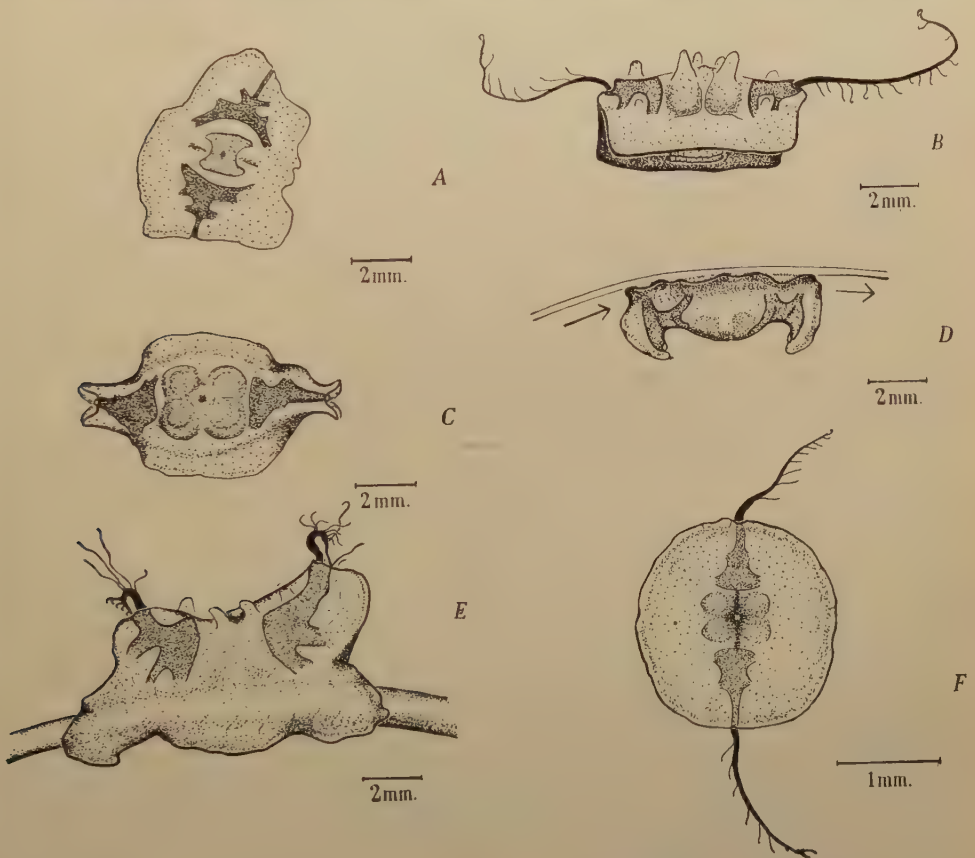


FIG. 1.—Drawings of living specimens showing typical changes in body form.

- A. Gliding phase, body very much shortened in oral-aboral axis.
- B. Floating position, showing folded body, extruded tentacles, aboral papillae, and oral lappets.
- C. Sitting position. Aboral view of specimen sitting on bottom of glass aquarium and showing chimney effect in tentacle region.
- D. Lateral view of folded specimen sitting on side of aquarium and showing groove through which current passes (indicated by arrows) and also arm processes.
- E. Lateral view of folded specimen sitting on algal filament, showing tentacular feeding and aboral papillae.
- F. Young specimen showing typical rounded outline and simplified tentacle sheaths. Specimen is resting under surface film and extruding its tentacles into water beneath.

which have flattened out to form an accessory creeping sole as seen in Pl. 3D and text-fig. 3E, F.

(c) *Floating phase.*

The animal occasionally loosens its hold on the substrate and floats away. It accomplishes this by folding its body along the tentacular axis and by shooting its tentacles in and out. Presumably the tentacles are extended so as to catch hold of a suitable algal or hydroid mass. As there are neither ctenes nor any other obvious organs of locomotion, this movement is probably due to the cilia of the oral surface and to the tentacles and so it is perhaps better to regard the animal in this phase as 'floating' instead of 'swimming'. In this form the oral grooves are shallow with the edges in the mouth region produced into marked oral lappets. The aboral papillae are usually fully extended and the 'anchor' shape of the tentacle sheath is clearly seen in this form. Pl. 2D and text-fig. 1B.

The shape of the animal when in this phase bears a close resemblance to that described by Dawydoff (1936) for *Coeloplana mesnili*.

(d) *Sessile phase.*

Vallicula is most frequently found in this form, usually sitting on a hydroid colony or algal filament as depicted in figs. 1E, 7B. It is folded along the tentacular axis with the central apical organ outermost and the portions of the body bearing the anchor-shaped tentacle sheaths folded and tilted upwards as chimney-like structures reminiscent of the 'arms' of *Lyrocteis* and the 'chimneys' of *Tjalpiella* (figs. 7C, D). In this position the animal may either extend its tentacles and actively capture prey or it may completely withdraw them and feed by means of the ciliary currents of the oral grooves. The oral lappets are partially extruded in this form.

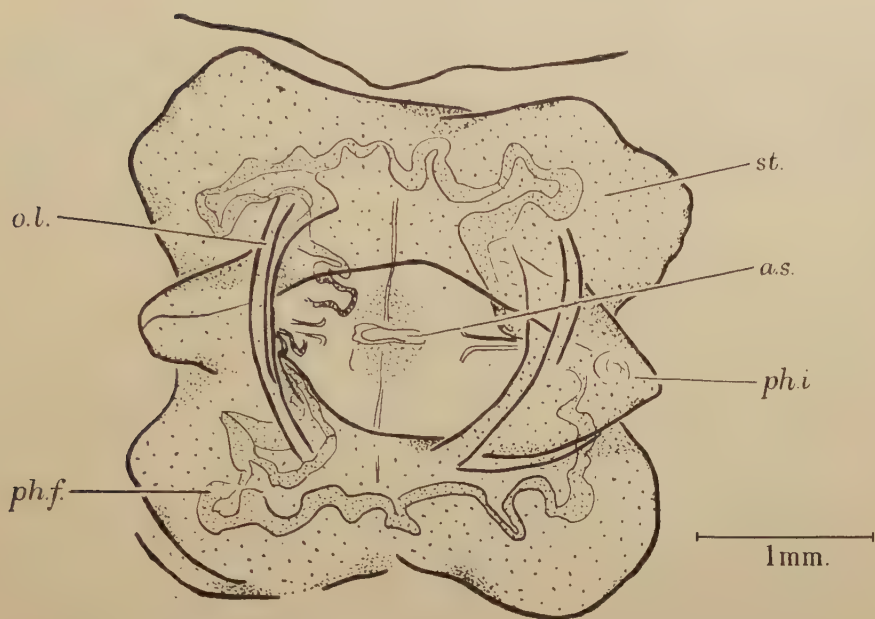
Tentacular apparatus.

The most obvious structures of the animal are its tentacles and each of these is housed in a tentacle sheath which differs somewhat in form from that of *Coeloplana* in that it has an additional 'cross-piece' (figs. 5, 7) into which tentacle filaments may be coiled. When the tentacles are fully extruded the tentacle sheath appears to alter its shape and to become more or less flask-shaped or even tubular. Careful examination, however, shows that the apparent alteration is due to the movement of the tentacular filaments out of the very thin-walled sheath, and that the actual shape remains the same. The typical 'anchor' shape is characteristic of mature specimens, whereas in very young forms (fig. 1F) the 'cross-piece' is only partially formed. The formation of the cross-piece is probably associated with the large number of tentacular filaments on the very long tentacle. The opening of each tentacle sheath is on the aboral surface and may even be curved well over the body of the animal in sessile phases (figs. 1D, 7B).

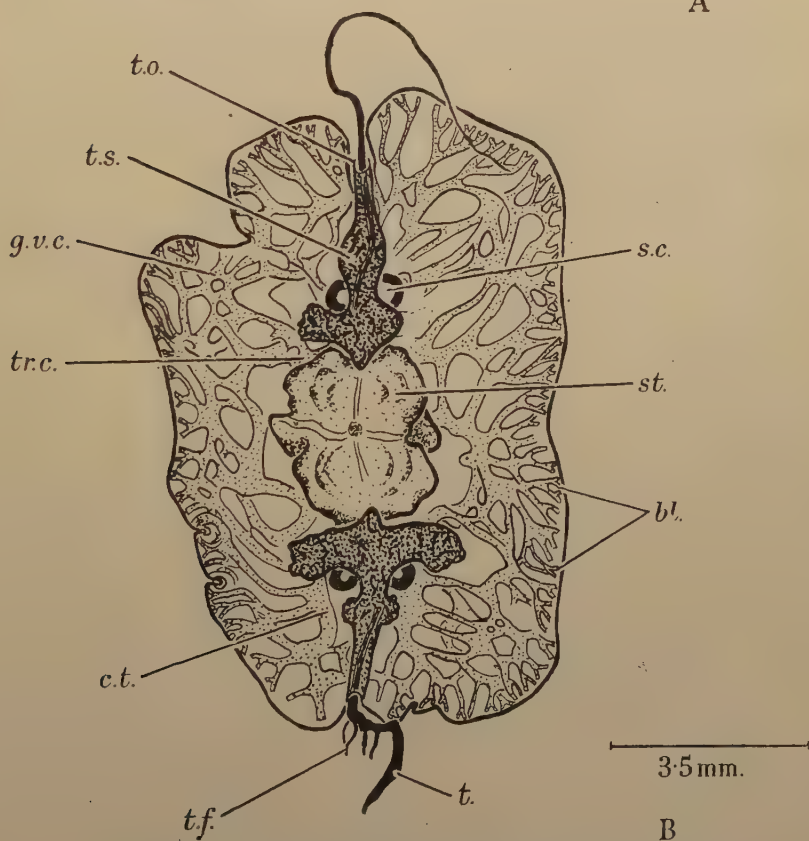
Each tentacle is composed of a tentacle base, a tentacle root, a tentacle stem and large numbers of tentacular filaments coming off from the tentacle stem in sequence and in more or less a straight line (Pl. 2A). Both the main tentacle and its filaments are highly contractile. The entire tentacle may be rapidly extruded and withdrawn and the individual tentacular filaments may also be contracted and extended singly. When the animal is disturbed the tentacles are quickly extruded and the tentacular filaments uncoil themselves in a 'shower' (Pl. 2A, D), adhering to any nearby structures. During normal feeding the tentacles may be extended to twenty or thirty times the length of the body, becoming extremely filamentous and difficult to see towards their distal ends. When a large number of specimens are actively feeding in an aquarium the general impression is of a tank full of fine gossamer threads weaving throughout the water.

Apical organ.

The apical organ is similar to that of other Ctenophores in that it possesses a dome-shaped chamber, an apical shelf, a statolith, and polar fields. Both the apical shelf and the roof of the dome are capable of opening and closing by muscular contraction, that of the dome somewhat resembling the contraction of a true sphincter,



A



B

FIG. 2.—Projection drawings of fixed, unstained specimen.

A. 'Mouth' region showing inner pharynx opening out and beginning to produce oral lappets. Same specimen as B.

B. Creeping phase, showing ramifications of gastrovascular system.

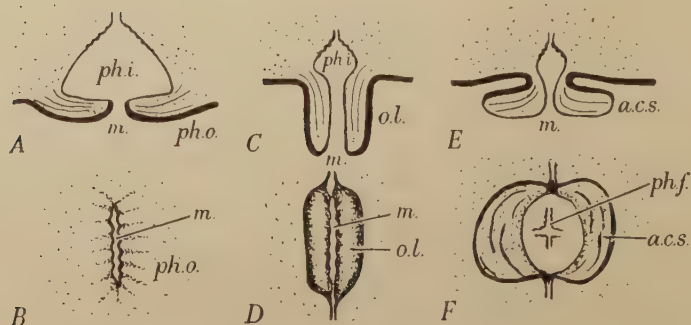


FIG. 3.—Diagram showing pharyngeal relations during production of oral lappets and accessory creeping sole.

- A. Lappets compressed, 'mouth' almost shut. Optical section.
- B. 'Mouth' with compressed lappets in oral surface view.
- C. Lappets extruded, 'mouth' open. Optical section.
- D. 'Mouth' with extruded lappets in oral surface view.
- E. Lappets produced outwards as an accessory creeping sole. Optical section.
- F. Oral surface view showing accessory creeping sole and oral grooves.

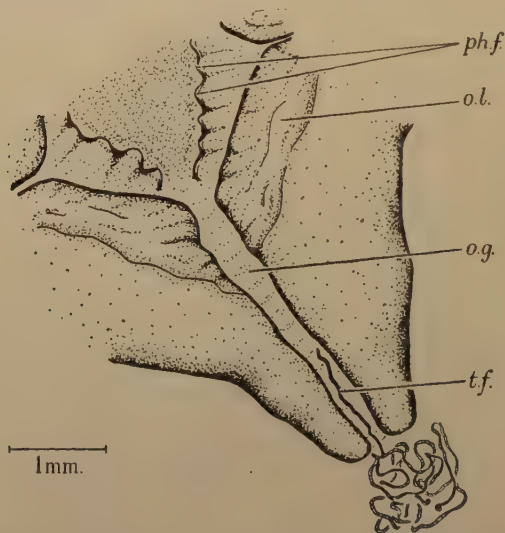


FIG. 4.—Drawing of oral view of furrowed arm as seen in phase contrast view of living specimen. Lappets are partially open. A tentacle filament is seen twisting round from aboral surface to wipe itself off in clearly marked groove.

as can be seen in fig. 6. The statolith is in the form of a concretion of small spherules and moves around over the long cilia of the apical shelf thus giving to the animal a sense of position. The polar fields are small and disposed, as indicated in fig. 6. The dome of the apical organ will also contract when touched or when chemically stimulated. Whether this is due merely to the inherent sensitivity of protoplasm or whether chemoreceptors, touch receptors or even proprioceptors are present is unknown. The animal is certainly particularly sensitive to external stimuli in this region.

Occasionally some pigment cells may be arranged in four definite tracts leading away from the polar fields in positions similar to the ciliated ridges of *Coeloplana* (Dawydoff, 1938).

Gastrovascular system.

The full relationships of this system have not as yet been worked out in the upper stomach region but the gastro-vascular pattern as a whole resembles *Ctenoplana* and is in other respects intermediate between *Cocloplana* and *Tjalfiella*. In spite of the transparency of the animal it is difficult to make out the parts of the gastro-vascular system without the aid of a phase-contrast optical system, as some parts are usually obscured by pigment.

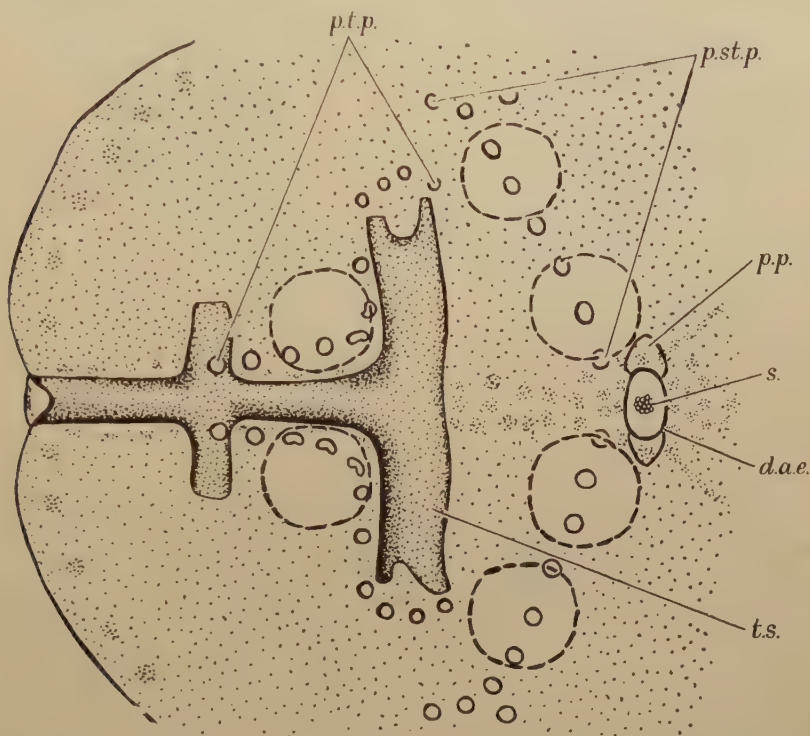


FIG. 5.—Plan of aboral papillae. Unbroken lines show arrangement when large numbers of papillae are present, broken lines show condition when few papillae are present.

The oral surface of the animal is the permanently everted outer pharynx and bears prominent oral grooves which lead into the 'mouth' at the entrance to the internal portion of the pharynx (Pl. 3D, and text-fig. 4), which is somewhat pyramidal in shape. As in other Platycetenids the 'mouth' is therefore the opening of the outer pharynx into the internal pharynx and is therefore not a morphologically true mouth although it serves the functions of one. The outer portion of the internal pharynx may in turn become everted in varying degrees to form oral lappets and an accessory creeping sole, as seen in fig. 3, depending on the phase of the animal.

The internal pharynx shows typical pharyngeal folds towards its innermost portion (fig. 2A) and these are divided into four groups (fig. 3) reminiscent of the condition in *Lyrocteis* (Komai, 1942). The inner pharynx opens into the oesophagus which is a flattened tube leading into the stomach (infundibulum). The stomach is large and somewhat sub-divided into four pouches (fig. 2A), from each of which is given off transverse canals, each pair of which is homologous with a split transverse canal of *Ctenoplana* (figs. 2B, 7B). Each of these transverse canals gives off one adradial and one tentacular, so that there are four adradials and two pairs of tentaculars in all. Almost at the junction of each transverse canal with its tentacular

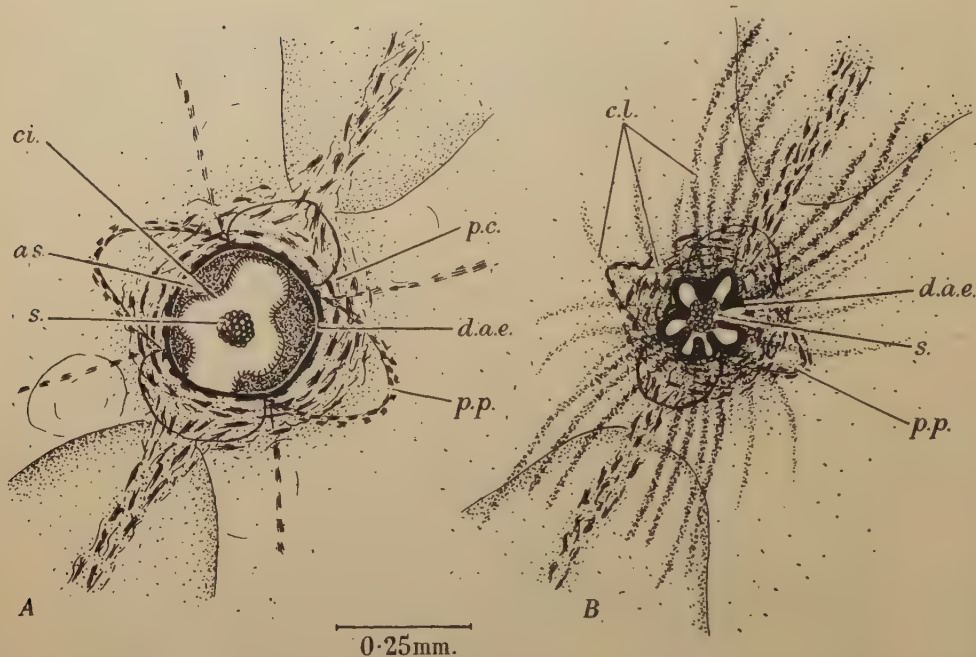


FIG. 6.—Drawing of apical region of living specimen showing opening and closing of apical organ.

A. Apical organ open, showing concretion of statolith and heavily ciliated apical shelf.

B. Apical organ closed, concretion barely visible and apical shelf now hidden.

canal is a large expansion of the sub-tentacular adradial canal, which is an almost spherical chamber with thickened walls and which can readily be seen in aboral view between the 'cross-piece' of the tentacle sheath and its basal portion (Pl. 3C, and text-figs. 2B, 7B). There are therefore four of these chambers. They are presumed to be genital in function, as small embryos have been seen swirling around within them, but further examination of microscopical sections is needed to determine the character of their thickened walls and to determine whether they are similar to the brood chambers of other genera.

In younger forms the basic canal pattern is more easily seen, as with increasing size the ultimate portions of the system become more and more branched and anastomosed. In Pls. 2D, 3B the basic pattern shows clearly in the living specimen under phase-contrast microscopy. Pl. 2D shows the general outline under low power and Pl. 3B shows a portion of the canal system of another specimen under high power. Fig. 2B is of a fixed, unstained specimen drawn under micro-projection and the increase in ultimate ramifications and anastomoses can be seen. The ultimate branches of the canal system are blind at all ages.

The aboral papillae are processes thrown out at intervals by the main gastro-vascular canals and are characterized by variability in shape and position, in direct contrast to the relative fixity of number and position of similar structures diagnostic of *Coeloplana* as noted in Dawydoff's review of the genus (1936). The papillae here may be numerous and small (fig. 5) or few and large (figs. 1B, 1E and 5) and each individual papilla when formed may alter its shape successively from conical to hemispherical, to digitiform, to lobed. There may be only four parastomal papillae in all, each being situated over a 'spherical chamber', and either eight parastomal papillae disposed over the transverse canals or four situated above the stomach pouches. This is usually the condition in the floating and sessile phases (fig. 1B, C), whereas in the creeping phase there is a tendency for a multiplicity of papillae arranged

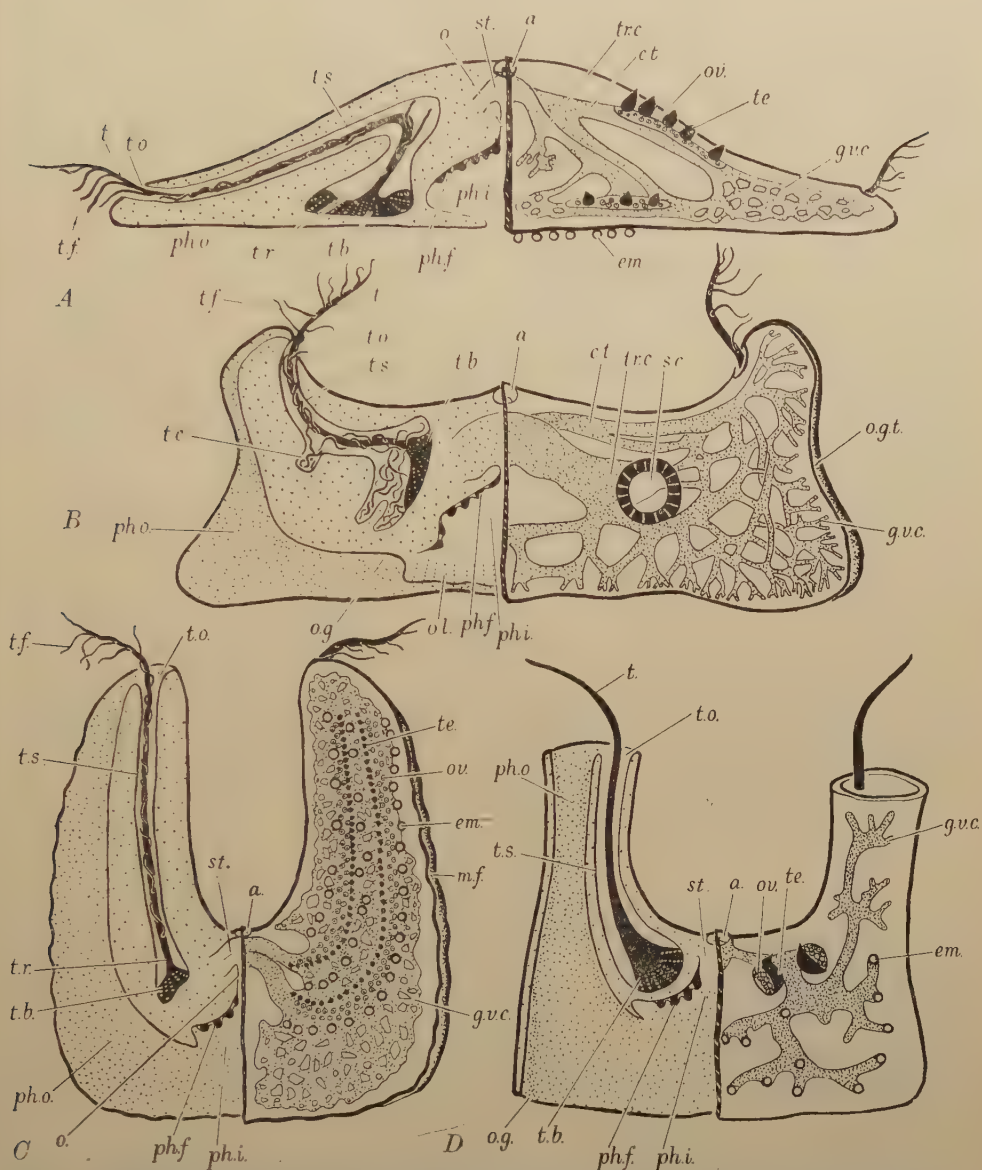


FIG. 7.—Diagram showing position of *Vallicula* in the morphological series of platyctenid ctenophores. All specimens in lateral view. *a*, *c* and *d* modified from Komai.

A. *Coeloplana*.

B. *Vallicula*.

C. *Lyrocteis*.

D. *Tjalfiella*.

as shown in fig. 5 with nine or ten parastomials on the transverse canals and ten or twelve paratentaculars on the tentacular canals. In all the papillae a rapid 'whirlpool' circulation of small particles can be observed.

FEEDING.

Small Crustacea, chiefly copepods and larval decapods such as zoeae, have been observed being caught by the colloblasts of the tentacles and transferred to the oral groove where, if they are sufficiently small to be carried in by the ciliary current,

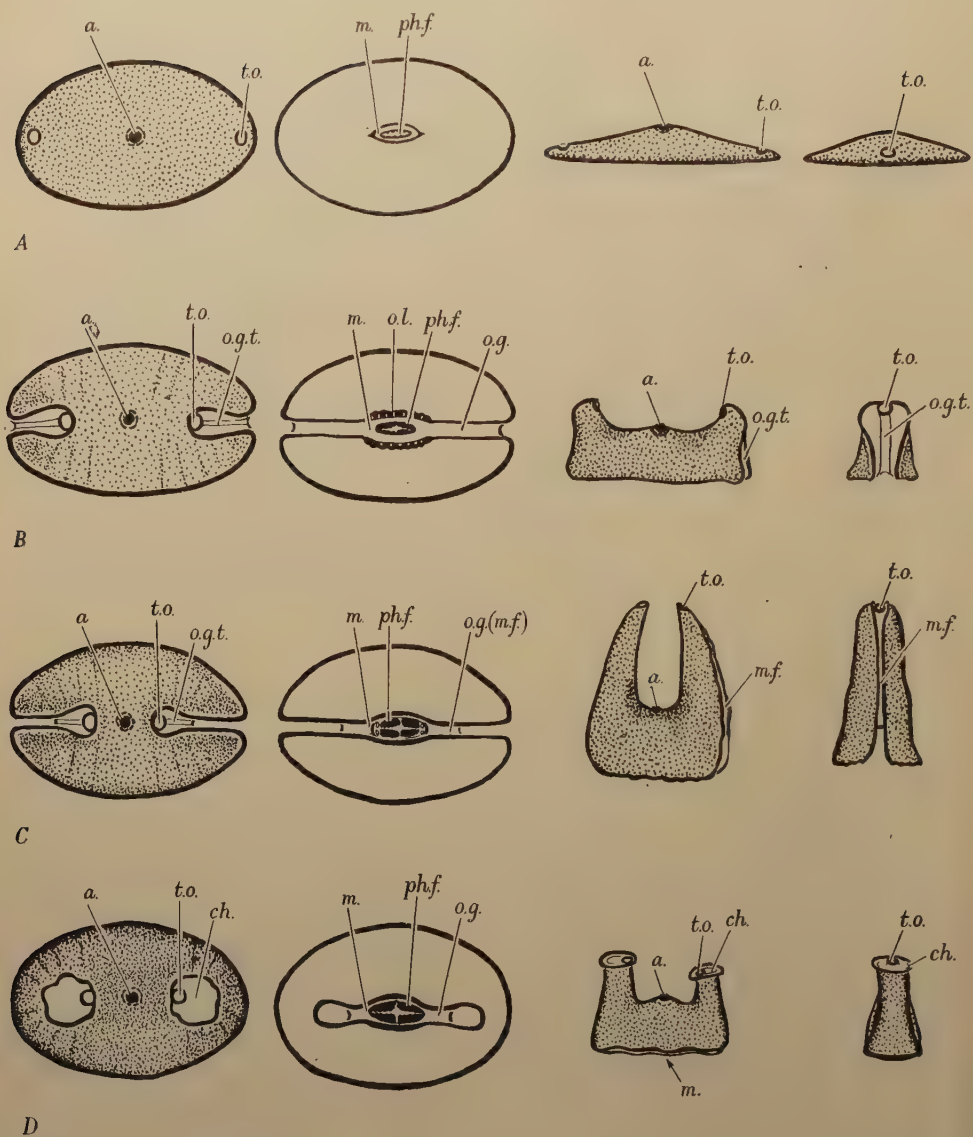


FIG. 8.—Diagram showing changes associated with the formation of the oral grooves in platyctenid ctenophores. All specimens are shown in aboral, oral, lateral and end-on views.
 A. *Coeloplana*.
 B. *Valticula*.
 C. *Lyrocteis*.
 D. *Tjalfiella*.

they may be wiped off by the tentacles (fig. 4) and thence passed through the 'mouth' to the inner pharynx. If they are very large they may be pushed into the inner pharynx by the tentacles, assisted by the contraction inwards of the oral lappets which act as lips. Occasionally tentacular filaments are broken off during this process and remain for a time moving about within the pharynx. The oesophagus, although narrow, is widely extensible, as large copepods are passed almost intact from the pharynx, into the stomach. Chains of diatoms have also been observed in the stomach pouches.

Experiments with iron saccharate and congo red show that unwanted particles are usually wrapped in mucous and ejected in balls or strands through the 'mouth', from whence they are usually passed over the oral lappets to the periphery and are passed out from under the animal and washed away.

Ciliary feeding appears to play a large part in the feeding mechanism of sedentary phases. Even with the tentacles completely withdrawn into their sheaths one can observe the movement of small particles inwards via the oral grooves to the 'mouth'.

RESPIRATION AND EXCRETION.

Vallacula is extremely sensitive to oxygen lack and soon becomes sluggish if the oxygen content of the sea water falls below the optimum. This can be demonstrated by placing six *Vallacula* (each of approximately one centimetre in length) in a two-gallon tank of sea water with a small piece of alga but without mechanical aeration overnight. After twelve hours they will have left the alga and will be found adhering to the glass sides of the tank and will be very sluggish. In another six hours they will probably start to disintegrate. The loosening of their hold from the alga is possibly an endeavour to move to a more suitable environment.

It is possible that the aboral papillae may play a part in the respiratory processes as they may not only serve to effectively increase the internal surface area for absorption of food particles from the rapidly swirling water within them, but may also ensure that only a thin layer of cells is between that water and the external medium. It is therefore a possibility that a correlation may yet be found between the size and number and position of these papillae and the oxygen content, as all these factors have already been shown to be variable.

No groups of excretory cells have yet been recognized and the mechanism of excretion has not yet been determined. At intervals temporary funnel-shaped folds are formed around the periphery and the cilia thus enclosed appear to beat more vigorously with an outward movement. It is possible that these temporary funnels may have an excretory function.

REPRODUCTION.

Vallacula is viviparous, shedding embryos which are almost ready to settle. These embryos have been observed in the spherical chambers and underneath the animal in the sessile phase or between the folds in the floating phase, but the details of their early development remain to be worked out. Newly settled specimens one millimetre in length have been observed and all of these show the juvenile characters mentioned previously.

SYSTEMATIC POSITION.

At present several genera, namely *Coeloplana*, *Ctenoplana* (including *Planoctena*), *Lyrocteis*, *Tjalpfiella* and *Gastra* are included in the order Platyctenida, but they do not all show the main characteristics designated to that group. Some characters are indeed so widely divergent from those of the designation that it is apparent that the order should now be redefined. The description includes in the Platyctenida all those ctenophores which are of a creeping habit, with body flattened in the principal axis, giving rise to an aboral and oral surface, with no meridional sub-costal canals, with a system of anastomosing peripheral vessels, with possible absence of comb-rows in the adult and the costae, when present, being retractile within ectodermal pouches, and with two retractile tentacles and sheaths.

An analysis of these features and a comparison of this description with the table of generic characters (Table I) bring out the following points. *Ctenoplana* is primarily a floating form and in it the flattening said to be characteristic of the order is not constant but only occurs at certain times. *Ctenoplana* and *Planoctena* (which was split off from the genus *Ctenoplana* by Dawydoff (1936) on the grounds of slight differences in the apical region and tentacle sheaths) are essentially pelagic free-swimming genera, the only exception being *P. caulleryi* which was collected from the octocorallian *Xenia*. *C. rosacea* and *C. Korotneffi* were also found in the

plankton, although creeping on a piece of floating cuttle bone, but the possibility remains that they crept onto the cuttle bone only while in the tow-net when normal conditions ceased. *Ctenoplana* thus cannot be termed as primarily a 'creeping form', although it is capable of assuming the flattened shape when the occasion demands. *Lyrocteis* and *Tjalfiella* are sessile animals and due to their structure it is unlikely that they are capable of doing more than loosening their hold on the substratum and allowing themselves to drift to a new abode. *Vallicula*, which shows many affinities to both *Coeloplana* and *Lyrocteis*, is predominantly also a sessile organism but has creeping and floating phases. Thus *Coeloplana* is the only predominantly creeping member of the order. One of its species, *C. mesnili*, has, however, never been observed to creep but is a planktonic form with the body folded in two along the tentacular axis and resembling the floating phase of *Vallicula*.

The only completely flattened member of the order is *Coeloplana* with the exception of *C. mesnili*. *Ctenoplana* on the other hand is only flattened when creeping and even then is not perfectly flat. The central part of the body remains hump-shaped with only the peripheral region, or 'skirt', becoming flattened due to eversion of the pharynx. The only other form which shows flattening is *Gastra*, but for many reasons, chief among them being the possibility that dissogeny may be occurring, as it so often does in other Ctenophora, its true position is problematical and it is not certain what form the final stage takes. *Lyrocteis* is not flattened, although the main axis of the body is somewhat shortened in the central region, and oral and aboral surfaces can be made out due to the eversion of the pharynx to form both an adhesive structure and a feeding groove. The projection of the body into two arms, which gives a lyre-shaped effect to the whole animal, is quite unlike anything found in either *Coeloplana* or *Ctenoplana* but resembles similar projections, 'chimneys', in *Tjalfiella* which may even be said to have developed one stage further. The arm-like processes of *Vallicula* are also reminiscent of these conditions in *Lyrocteis*, although they are very much shortened. *Tjalfiella* also is not flattened but rather shortened in the oral-aboral axis in the central region of the body.

The statement that there are no meridional subcostal canals in Platyctenids is also misleading. Their homologues are almost certainly present in all members of this group, although they are altered either in shape or relative position due to the modifications of general body form. In *Ctenoplana* it is obvious that each of the two transverse canals gives rise to four adradial and two tentacular canals, the distal end of each transverse canal being somewhat split into two so that one tentacular and one adradial canal comes off from each half. The interradials are missing (although they could possibly be said to be represented by the split portions of the transverse canals) and the adradials merge immediately into the anastomosis of peripheral canals. The gonads, as far as they have been described, appear to come off the adradial canals near their branching into the meridional canal anastomosis. On further investigation it is not unlikely that the gonads will be found to extend down to the proximal part of the meridional anastomosis, thus conforming to the typical ctenophore pattern.

In *Coeloplana* the position is even clearer, as the two transverse canals give off directly eight adradial canals which branch immediately into recognizable meridional vessels which in turn proceed to branch profusely until an anastomosing system is formed. The gonads are found on the meridional canals. In *Lyrocteis* again the meridional canals can be traced by the presence of the genital diverticula, whereas in *Tjalfiella*, due to considerable shortening of the main axis of the body, these diverticula are found on the very much reduced meridional vessels located at the ends of the adradial canals, the interradials again being missing. In *Vallicula* the gonads have not definitely been recognized, nor have the true relations of the spherical chambers been sufficiently sorted out to warrant discussion, but the general canal pattern appears to resemble that of *Ctenoplana* with its missing interradials and split transverse canals. In all Platyctenids the tentacular canals are bifid, a ramus running down each side of the tentacle sheath,

TABLE I.—Comparison

	<i>Ctenoplana</i> *	<i>Coeloplana</i>	<i>Vallic</i>
LOCALITY	West Coast of Sumatra Bay of Nhatrang, South Annam Eastern archipelago of New Guinea Bay of Bengal, off Madras Gulf of Manaar French Indochina Palestine	Red Sea Misaki, Japan Coast of Annam Netherland Indies Spice Islands Gulf of Siam	Palisadoes,
HABITAT	Plankton	On <i>Sargassum</i> , <i>Alcyonium</i> <i>Krempfi</i> , <i>Dendronephthys</i> , <i>Simularia</i> , <i>Pennatula</i> , <i>Ptero-</i> <i>eides</i> , <i>Posidonia</i> , <i>Heterocen-</i> <i>trotus mammilatus</i> , <i>Toxop-</i> <i>neustes</i> , <i>Solenocaulon</i> at 20 metres, <i>Echinaster lugonicus</i> at 15 and 25 metres	In shallow <i>nigra</i> Sav hydroids, <i>fera</i> , <i>Cau</i> Plankton
HABIT	Swimming, occasionally creeping	Creeping (except. <i>C. mesnili</i>)	Floating predomina
BODY FORM	Central portion helmet-shape, peripheral region flattened when creeping	Body flat, except in <i>C. mesnili</i> which is folded in two along tentacular axis	Folded in tw axis with prolonged sometimes
SIZE	3 to 8 mm. along tentacular axis, 2 to 3 mm. height	5 to 60 mm. along tentacular axis	1 to 13 mm axis
COLORATION	Brightly coloured with greens, reds or browns	Brightly coloured with reds, brown, yellows, violets, greens	Transparent sionally pa
COMB PLATES	Present in adult, retractile within ectodermal pouches	Absent in adult	Absent in a
APICAL ORGAN	Well developed, with papillae in polar fields	Well developed, with papillae in some species and ciliated bands	Well devel and polar bands, no
TENTACLES	Pinnate, retractile	Pinnate, retractile, 6 to 20 times length of animal. <i>C. sophiae</i> only four times	Pinnate, re times lengt
TENTACLE SHEATHS	Flask-shaped in aboral view, opening on aboral surface	Flask shaped in aboral view, opening on aboral surface	Anchor-shap opening at
PHARYNX	Everted and flattened out only when creeping	Permanently everted and flattened out to form 'oral surface', except <i>C. mesnili</i> . With trace of oral groove in <i>C. sophiae</i>	Everted an when cre further eve lappets or sole. Oral
GASTROVASCULAR SYSTEM	Meridional canals branched, forming anastomosis. Bifid tentacular canals No aboral papillae	Meridional canals branched and anastomosed. Paired tentacular canals Aboral papillae with fixed number for each species	Meridional and anaste tentacular Aboral pap shape, num
GONADS	Ovary unknown Compact sperm masses with ducts to exterior	Ova in continuous linear tract from each meridional canal Compact sperm masses with ducts to aboral surface Seminal receptacles (?) present	Gonads not Spherical cl brood chan
DEVELOPMENT	Cydippid larva	Cydippid larva Broods young	Cydippid lar Broods youn

* includes *Planoctena*.

ers in the Platyctenida.

<i>Lyrocteis</i>	<i>Tjalfiella</i>	<i>Gastra</i> (= <i>Gastrodes</i>)
Sagami Bay off Enosima, Japan	Umanak Fjord West Greenland	Mediterranean
On gorgonids at 70 metres	On <i>Umbellula Lindahlii</i> K��ll. at 475 to 575 metres	In <i>Salpa fusiformis</i> and <i>Salpa confederata</i>
Sessile	Sessile	Said to be parasitic
Body lyre-shaped, with long arm-like processes and open marginal furrow	Body squat with ends prolonged into 'chimneys'	Shape of inverted saucer
10.8 to 13.8 cm. from tip of arm to margin of trunk	Total height at chimney 10 mm. Width across body 20 mm.	'Minute'
Brightly coloured in yellows, pinks, greens	Transparent, colourless	—
Absent in adult	Absent in adult	Absent in most mature stage yet found
Rather small, no papillae	Rudimentary, no polar fields, ciliated bands, dome or papillae	—
Pinnate, retractile, up to 60 cm.	Unbranched, short	Rudimentary
Elongate, tubular, opening at tips of arms	Tubular, bulbar at base, opening within chimney	Juvenile appearance
Everted, not flattened, forming marginal furrow in arms with apposing edges	Everted, turned up into two 'chimneys'	Everted in last known stage
Meridional canals much branched and anastomosed No aboral papillae	Meridional canals reduced No anastomosis	Meridional canals are broad sacs
Ovaries in diverticula of meridional canals Testes in diverticula of meridional canals each with ducts to exterior Seminal receptacles (?)	Ovaries at ends of meridional canals Testes near ovaries, no ducts to exterior Seminal receptacles (?) present	Ova in wall of 'ventral' surface Testes unknown
Cydippid larva	Cydippid larva Broods young	Planula then cydippid

Anastomoses of the peripheral vessels of the gastro-vascular system occur in all Platyctenida with the exception of *Tjalpiella*, where the ultimate branches are few in number, and *Gastra* where the maturity of the largest known specimen is still in doubt. *Lyrocteis* has the most intricate meshwork, possibly correlated with the extraordinary bulk of the animal, whereas the remaining members of the group have a less complex arrangement. Branching and anastomoses of the meridional canals are not restricted to the Platyctenids but are also found in the Beroida where at least the ultimate branches in the mouth region anastomose to form a circum-oral canal, and in some cases a network is found throughout the length of the meridional canals. In Lobata these canals do not branch throughout their length but do form anastomoses around the mouth and oral lobes.

It is interesting to note that only in *Ctenoplana* are the comb-rows, characterized by being retractile into ectodermal pouches, present in the adult. The most mature stage yet recognized in *Gastra* has been observed to cast off its ctene rows, but it is not yet certain whether this is a normal occurrence.

The presence of two retractile tentacles and sheaths is a constant feature, but is also one which is shared by the order Cydippida.

Thus it can be seen that the designation of the order is inaccurate. An alternative which would fulfil all the requirements is rather difficult to find, as there is such diversity of characters within the group. There are, however, the following features which all members possess in common: (1) body shortened in oral-aboral axis, (2) pharynx modified with oral portion permanently or temporarily everted to form creeping, adherent or ciliary feeding organ, (3) meridional canals either reduced or branched and or anastomosed, (4) tentacular canals bifid or paired, (5) ctene rows usually absent in adult costae, when present, retractile into ectodermal pouches, (6) tentacles two in number, both with sheaths, and (7) usually viviparous.

With regard to the first feature it is preferable to use the word 'shortened' instead of 'flattened', for, as previously indicated, true flattening can only be said to occur in *Cocloplana* (except *C. mesnili*) and in *Gastra*. The extent of the shortening is also very variable within the group. That shortening of the main axis has in fact taken place is mentioned by Mortensen (1912), who points out that the infundibular canal is reduced and the anal canals (excretory canals) proceed directly from the infundibulum or stomach. The term 'flattening' is therefore merely an ambiguous method of describing the eversion of the pharynx.

The eversion of the pharynx is characteristic of all genera, although its ultimate function may vary. This character is also shared by the Cydippid *Lampetia* but other features such as the lack of branching meridional canals suffice to distinguish it from the Platyctenids.

The branching of the meridional canals of the gastrovascular system occurs also in the beroids but they are readily distinguished from the platyctenids by reason of their bodies being elongate in the oral-aboral axis and by their complete lack of tentacles.

The fact that the tentacular canals are bifid or even paired seems to have been previously overlooked, but from a careful comparison of descriptions and text-figures it would appear to be a constant feature of the Platyctenida.

The presence of the costae with retractile ctenes is a cydippid feature which persists only in the adult *Ctenoplana*, but this animal is not likely to be confused with the Cydippida owing to its anastomosis of meridional canals. The presence of two tentacles with sheaths is also a characteristic of the Cydippida, but as it is a constant feature of the Platyctenida it seems advisable to retain it in the diagnosis, unless a super-order, the Bitentaculata, were to be constructed to contain the two orders with this characteristic.

The proposed new genus *Vallicula* displays, together with all the other members of the Platyctenida, the above listed features. It thus has a shortened body, an everted pharynx, branched and anastomosed meridional canals, paired tentacular canals, no ctene rows, two tentacles with sheaths, and is known to brood its young.

It can be distinguished from *Ctenoplana* by the complete absence of ctenes in the adult, and from *Gastra* for the same reason, together with its complex gastrovascular system. It shares with *Coeloplana* the aboral papillae but lacks the constancy in number and position which *Coeloplana* shows. It also resembles *C. sophiae* in that it possesses an oral groove and *C. mesnili* in that it is capable of folding the body in two along the tentacular axis. *Vallicula* may, however, be distinguished from all *Coeloplana*, including these two species, by the possession of three phases of body form, the anchor-shaped tentacle sheaths, the spherical chambers, the elongate tentacles and the oral lappets. *Lyrocteis* and *Tjalfiella* may also be distinguished from *Vallicula* by the presence of elongate 'arms' and 'chimneys' respectively, and also by the fact that *Vallicula* retains the powers of floating and creeping.

It is therefore necessary to erect a new genus for the reception of this form. Only one species of this genus has as yet been recognized, the three main colour variations which might be expected to be specific being apparently interchangeable and dependent on the immediate surroundings. The features which will probably be found to be of specific variability are the disposition and character of the pigmented areas and the transparency of the animal. Owing to the variability of number, shape and position of the aboral papillae it was considered impossible to regard this feature as being of specific value as has been done in the case of *Coeloplana*. It is not possible to go further than this at the moment so it has been thought best to describe the minutiae of the present form as characteristic of *V. multiformis*.

Diagnosis of Vallicula, gen. nov.

Gregarious. Body shortened in oral-aboral axis, with pharynx extended for creeping on the oral surface, or body folded in two along the tentacular axis and floating, or similarly folded and sessile on brown algae, hydroids or ascidians. Comb plates absent. Oral grooves extending from 'mouth' along tentacular axis to openings of tentacle sheaths on aboral surface, with oral edges in central region either produced as a pair of lappets, or further extended to form an accessory creeping sole, or compressed and furrowed, almost closing the 'mouth' opening. Oral grooves bent upwards in arm-like projections of the body produced in floating and sessile phases. Anchor-shaped tentacle sheaths with extensible tentacles up to twenty or thirty times the length of the body and bearing branchlets with colloblasts. Branching and anastomosing gastro-vascular system with aboral papillae capable of altering their position and shape, and with two well-marked spherical chambers near each tentacle sheath.

Diagnosis of V. multiformis, sp. nov.

Transparent, either colourless with whitish markings or lightly coloured on aboral surface with brown, pink or green pigment, colour being most pronounced in area immediately surrounding apical organ, along tentacular axis and around periphery, red pigment occurring in small globules, green and brown in cells resembling chromatophores.

It is therefore clear from a survey of the Platyctenida that there is a series of genera which vary from free-swimming to sedentary forms, and which also show the progressive flattening and grooving of the outer pharynx and its eventual formation into chimneys with the associated phenomenon of the gradual increase in capacity for ciliary feeding. Komai (1942) pointed out the resemblances of *Lyrocteis* to both *Coeloplana* and *Tjalfiella*. It is now apparent that *Vallicula* forms an additional link in the series (figs. 7 and 8). Since the sedentary forms are the most highly organized it would appear that there has been a definite progression towards this mode of life. *Vallicula* therefore appears to provide confirmatory evidence for the modern theory that the Platyctenida are merely an extremely specialized offshoot of the Ctenophore stem and not intermediate between Ctenophora and Platyhelminthes (see Komai, 1922). It can be seen from a consideration of the

above description that the creeping habit is a transitory phase in the change-over from free-swimming to sessile habits and not merely an end-point in itself. Thus in the one animal, *Vallacula*, can be seen the way in which this change can be brought about, for in its various phases it is at one time floating, at other times gliding and creeping or sedentary. In the sessile phase can also be seen the change in the pharyngeal region with the production of a very deep groove capable of assisting in ciliary feeding.

Therefore with the discovery of *Vallacula* we now have eight stages in the transition from free-swimming to sessile habits in the Ctenophora. The first in the series is the cydippid ctenophore *Lampetia* and it is perhaps worthy of note that the order Cydippida is the least modified order of the ctenophore phylum. *Lampetia* is capable of everting its pharynx and using it as a creeping sole, although it is a typical, free-swimming cydippid (Komai, 1934; Hyman, 1940). Mortensen (1927) expressed doubt that the portion used by *Lampetia* for creeping was homologous with the outer pharynx of platyctenids, but it is now generally agreed that it is in fact homologous.

The second stage is seen in *Ctenoplana* which at times retains the ctenes, the helmet shape and the pelagic habit, but is also capable of settling down with everted pharynx and creeping over the substratum. Gnanamuthu & Nair (1948) state that the pharynx forms "nearly half the height of the animal" when not everted. *Coeloplana mesnili* shows the next stage with retained helmet shape and presumed capacity to evert the pharynx but with loss of the ctenes (Dawydoff, 1938). Other species of *Coeloplana* have never been reported as showing the free-swimming phase in adult life but apparently show only the creeping habit, many being found in deep-sea dredges. *C. sophiae*, described by Dawydoff (1938) from a single specimen, shows in addition the development of a groove running across the oral surface of the animal in the tentacular axis and with the 'mouth' in the centre. In *Vallacula*, the next stage, the animal shows in its various phases the helmet shape, the creeping form, a deepened groove, oral lappets or an accessory creeping sole, and finally an upward tilting of the tentacle sheaths and external pharynx to form furrowed arms. In *Lyrocteis* these processes or arms seem to be more permanent and the sessile phase is the only one yet found in the adult stage. *Tjalsiella* completes the series by having the arms rounded off into chimneys and by a reduction of its tentacles, with complete loss of tentacular filaments, so that obviously feeding must take place by ciliary mechanisms in the chimneys.

The parasitic *Gastra* (= *Gastrodes*) is, as mentioned previously, still incompletely known, and it is possible that the 'parasitic' stages are making use of an ingenious method of transport to new grounds and that the truly adult stage will yet prove to be sessile.

Another platyctenid bearing a general resemblance to *Coeloplana* has been found in Florida waters (Smith, 1945) but is still undescribed, and it is therefore not known whether it is a new species of *Coeloplana* or a new genus.

SUMMARY.

A new genus of platyctenid Ctenophore is described and is shown to be intermediate in structure between *Coeloplana* and *Lyrocteis*. It is shown to form a further step in the series from free-living to sessile forms, and to furnish additional proof that the Platyctenida are specialized offshoots of the ctenophore stem and not intermediate between Ctenophora and Platyhelminthes. A new definition of the order Platyctenida is given.

ACKNOWLEDGMENTS.

I am indebted to Professors C. Dawydoff and the late Th. Mortensen for encouragement in pursuing this identification; to Drs. T. Komai and Velappan Nair for information and helpful advice; to Dr. L. Hyman for examining specimens and comparing them with other genera available to her, including the undescribed form

from Florida; to Mrs. E. Robertson for identifying the algae; to Mr. G. Underwood for helping with the photography; to Professor N. Millott for placing laboratory facilities at my disposal; and to Dr. Pantin for helpful advice.

ILLUSTRATIONS.

PLATE 2.

Photographs of living specimens of *Vallicula*.

- A. Living specimen creeping on bottom of glass aquarium and extruding tentacles after gentle irritation.
- B. Living specimens crawling over tests of *Ascidia nigra* Savigny, in aquarium.
- C. Phase contrast photomicrograph of young specimen taken on slow plate to show characteristic turning movement used often when gliding over a flat surface. One tentacle is partially extruded to act as a rudder. Animal is turning in a clockwise direction.
- D. Phase contrast photomicrograph of floating specimen in plastic sea-water cell showing typical folded position. The tentacle on left is being rapidly extruded in a shower. Disposition of pigment and branched canal system also visible.

PLATE 3.

Specimens of *Vallicula*.

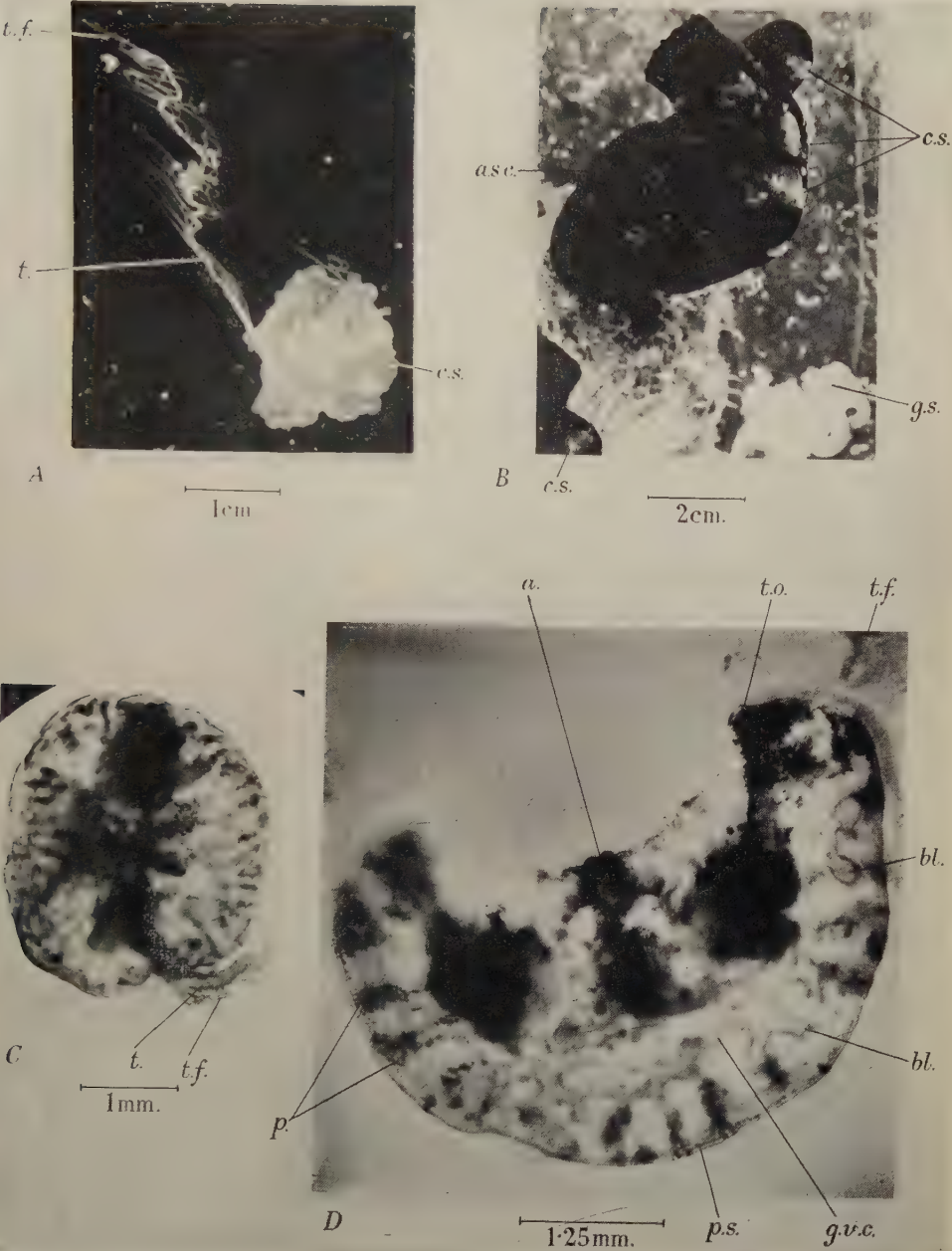
- A. Phase contrast photomicrograph of gliding specimen in surface view to show disposition of pigment.
- B. Phase contrast photomicrograph of peripheral region of gastrovascular canal system of young specimen.
- C. Photograph of tentacle sheath with almost fully extended tentacle. Fixed, unstained specimen.
- D. Photograph of oral view of creeping specimen showing oral grooves and accessory creeping sole.

KEY TO LETTERING OF TEXT-FIGURES.

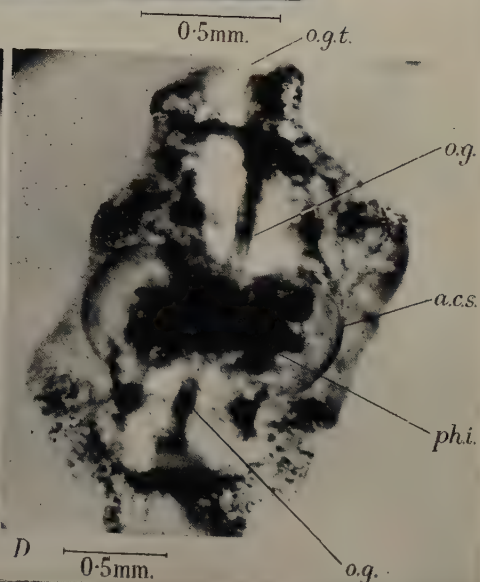
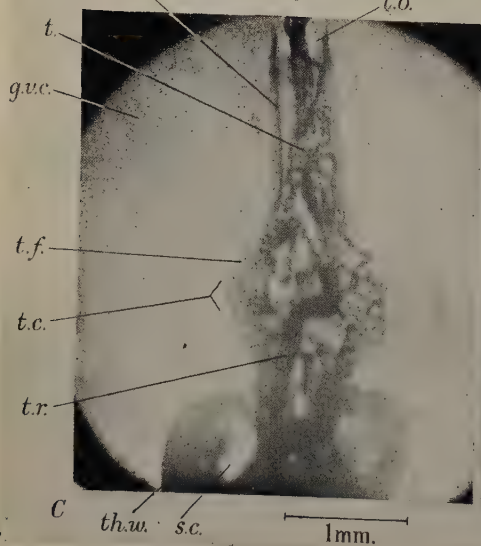
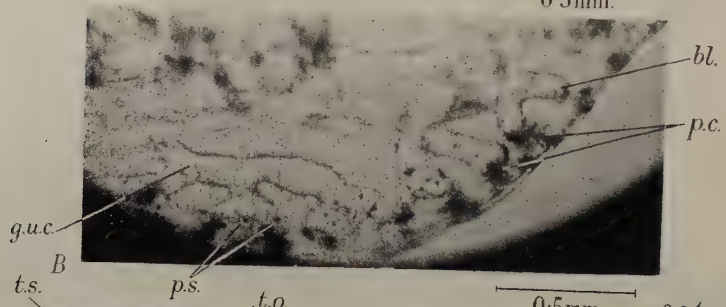
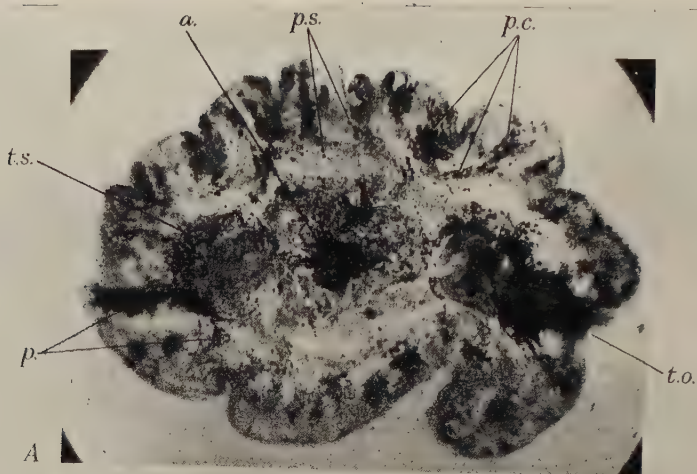
<i>a.</i>	= apical organ.	<i>o.l.</i>	= oral lappet.
<i>a.c.s.</i>	= accessory creeping sole.	<i>o.t.</i>	= ovarian tract.
<i>as.</i>	= apical shelf.	<i>ov.</i>	= ovary.
<i>asc.</i>	= ascidian.	<i>p.</i>	= pigment.
<i>b.c.</i>	= brood chamber.	<i>p.c.</i>	= pigment cells.
<i>b.l.</i>	= blind ends of peripheral canals.	<i>ph.f.</i>	= pharyngeal folds.
<i>c.f.</i>	= cross-furrow dividing pharyngeal folds.	<i>ph.i.</i>	= internal pharynx.
<i>ch.</i>	= chimney.	<i>ph.o.</i>	= external pharynx.
<i>ci.</i>	= cilia.	<i>p.s.</i>	= pigment spherules.
<i>c.l.</i>	= contraction lines of dome muscles.	<i>p.st.p.</i>	= parastomial papillae.
<i>c.s.</i>	= creeping specimen.	<i>p.p.</i>	= polar plate.
<i>ct.</i>	= tentacular canal.	<i>p.t.p.</i>	= paratentacular papillae.
<i>d.a.</i>	= dome of apical organ.	<i>s.</i>	= statolith.
<i>d.a.e.</i>	= peripheral edge of dome of apical organ.	<i>s.c.</i>	= spherical chamber.
<i>d.p.</i>	= aboral papillae.	<i>st.</i>	= stomach.
<i>em.</i>	= embryo.	<i>t.</i>	= tentacle.
<i>g.s.</i>	= gliding specimen.	<i>t.b.</i>	= tentacle base.
<i>g.v.c.</i>	= gastrovascular canals.	<i>t.c.</i>	= 'crosspiece' of tentacle sheath.
<i>in.</i>	= infundibulum.	<i>te.</i>	= testis.
<i>m.</i>	= 'mouth'.	<i>t.f.</i>	= tentacular filament.
<i>m.f.</i>	= marginal furrow.	<i>th.w.</i>	= thickened wall of spherical chamber.
<i>o.</i>	= oesophagus.	<i>t.o.</i>	= opening of tentacle sheath.
<i>o.g.</i>	= oral groove.	<i>t.r.</i>	= tentacle root.
<i>o.g.t.</i>	= oral groove curving round to opening of tentacle sheath.	<i>tr.c.</i>	= transverse canals.
		<i>t.s.</i>	= tentacle sheath.
		<i>t.t.</i>	= testicular tract.

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VALLICULA MULTIFORMIS.



VALLICULA MULTIFORMIS.

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SYSTEMATIC AND ECOLOGICAL NOTES ON THE CLADOCERA OF LAKE TOBA, AND THE SURROUNDING COUNTRY, NORTH SUMATRA.

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(With 6 text-figures.)

[Read 21 October 1954.]

INTRODUCTION AND TOPOGRAPHY.

This paper is based on the results of a month spent collecting on the eastern shores of Lake Toba. This lake is a fairly ancient and isolated tectonic lake occupying a large depression in the Batak plateau region of North Sumatra. It is by far the largest lake in Indonesia, and is indeed one of the largest lakes in South-east Asia. Lying at a height of 910 metres above sea-level, it covers an area of 1129.7 square kilometres and has a maximum depth of at least 433 metres. The lake is divided into two principal basins and several minor basins. Prapat (see fig. 1), which was my main collecting centre, lies near the southern end of the northern basin. The map also shows the positions of Balige, Porsea, and Pangururan, which were the principal stations from which the Deutsche Limnologische Sunda-Expedition operated. The surrounding plateau lies for the most part at an altitude of over 1,200 metres, and normally the slopes bounding the lake are almost precipitous. In a few regions, as near Prapat, Balige, Porsea, and Pangururan, small plains open unto the lake and there are areas with a somewhat sheltered littoral zone. Even in these places there are few or, as at Prapat, no extensive reed-beds, though there is commonly some submerged and floating vegetation. Published records indicate that the pH of the lake-water is high (often over 8.0 at the surface), and the alkalinity is about 73 mgm. of calcium carbonate per litre.

On the basis of these physical features, the lake would be classed, in temperate regions, as of either alkaline oligotrophic or mesotrophic type. The usefulness of such a classification is rather doubtful when applied to a tropical lake. The absence of a true thermocline makes a direct comparison with equivalent temperate lakes rather difficult. A safer and less misleading description is to class Lake Toba as a little-evolved alkaline lake.

The littoral fauna is of the rather sparse 'insectan' type characteristic of such lakes. It is dominated by Ephemeroptera, free-living Trichoptera, Plecoptera and sponges. Several species of snails do occur but are nowhere dominant and only important in favourable areas. Both the littoral and planktonic algae are reminiscent of those found in mesotrophic lakes in Europe. At the time of my visit, the Phytoplankton consisted largely of *Botryococcus*, *Microcystis* and *Coelosphaerium* with some diatoms, but no constituent was at all abundant. The littoral algae consisted largely of diatoms and Chlorophyceae. The only common Myxophycean was a form of *Gloetrichia*, a genus which is often found in comparatively little-evolved lakes. The biota thus supports the conclusions based on the physical and chemical characteristics of the lake.

The area has a typical tropical climate modified by its altitude and by the effects of cool winds from the surrounding plateau. Thus the water-temperature of the lake is never very high. The Deutsche Limnologische Sunda-Expedition determined the temperature at the water-surface of the main basins as varying between 25.5 and 27° C. during March and April.



FIG. 1.—Sketch map of Lake Toba, North Sumatra.

The region is a rain-shadow area and has a pronounced dry season in July to August (the period of my visit). During the first three weeks of my visit the rainfall was nil. Thus many of the small water-bodies are shallow and more or less impermanent. The only fully permanent water-bodies, apart from the lake, in the region of Prapat were an artificial pond on the peninsula and the inner part of the marshes in the South Bay. All these small water-bodies were ordinary small ponds. They were mostly slightly acid, as was indicated by the presence of desmids and *Chroococcus* but not markedly so. The habitats from which collections were made by the German expedition were more varied, though all small. They included some very acid solfataras near Pangururan and the rather extensive marshes in the region of Balige. Apart from such small water-bodies the area has no standing water other than the lake itself. Thus the collections of the expedition and my collections should when taken together give a representative picture of the fauna of the region.

Previous reports on the fauna of the lake have been given by Richard (1895), who was mainly concerned with the planktonic species, and by Brehm (1933), who reported on the extensive collections of the Deutsche Limnologische Sunda-Expedition. My collections were mainly from the littoral region, though I did not

completely ignore planktonic forms. For purposes of comparison I have given in Table I a complete list of the species recorded by Brehm, and those occurring in my collections. Some of the differences between these two lists are to be explained by the fact that my collections were from a more restricted area, and did not include any large samples of the plankton. Even allowing for this, the divergences between the two lists appear to be very large. This is probably due to the general rarity of most of the littoral species, apparent in Brehm's records as well as in mine. In such a situation random collecting, unless both very intensive and extending over a considerable period of time, is likely to overlook a considerable proportion of species. In this situation it is gratifying that the two lists taken together give a local fauna list which is comparable to that of other South-east Asian localities, and shows remarkably few special features.

The apparent isolation of the Toba basin seems to have had little effect on its Cladoceran fauna. There is only one endemic species, *Diaphanosoma modigliani*. The fauna does not appear to be greatly restricted. It is true that no species of *Daphnia* or *Moina* have been found in the main lake; but this is consistent with the general little-evolved nature of the lake. The littoral Cladocera show a variety quite comparable with those of adjacent areas, and, where species have not been recorded, this is almost certainly either the result of chance omissions in collecting or, as the absence of *Pseudosida*, due to the lack of suitable habitats.

The Cladoceran fauna of the Toba region consists predominantly of widespread species. As with the faunas of other South-east Asian localities these fall into two major categories: (a) species with an essentially pan-tropical distribution, including *Diaphanosoma sarsi* (= *excisum*), *Scapholeberis kingi*, *Ceriodaphnia cornuta*, *Macrothrix triserialis*, probably *Macrothrix spinosa*, *Ilyocryptus halyi*, *Alona glabra*, *A. verrucosa*, *A. karua*, *A. davidi*, and *Chydorus barroisi*; (b) species which are almost or completely cosmopolitan in distribution including *Simocephalus vetulus*, *S. exspinosus*, *S. serrulatus*, *Ceriodaphnia dubia*, *Alonella excisa*, *Chydorus sphaericus*, *Pleuroxus aduncus*, and probably *Leydigia leydigi*.*

The specifically Oriental element in the fauna is very restricted. The only species which can be assigned to it with any degree of certainty are: *Latonopsis australis*, *Macrothrix sumatrensis*, *Euryalona orientalis* and possibly *Macrothrix tobaensis*. It is of interest that the two characteristically northern species *Daphnia longispina* and *Acroperus harpae* are not recorded from this area, though both occur in Sumatra, and, according to Brehm, the latter is abundant at high altitudes (above 1500 m.).

NOTES ON STATIONS.

Station I. Batak village on North side of Prapat Bay, 12 August 1953. Moderately exposed; gravelly bottom; with *Myriophyllum* beds. Collection by throwing-net and washings of *Myriophyllum*. Associates: young fish; a few insect larvae; a single *Diaptomus*, etc. Algae, etc.: algae sparse, mainly filamentous and also epiphytic diatoms. Some detritus. Species collected: *Alona*? *intermedia*; one specimen only obtained.

Station II. North side of Prapat Bay, outside Prapat village, 18 August 1953. Shore very steeply shelving; rocks, etc., clothed with *Myriophyllum* and some *Potamogeton* (of submerged type), slightly sheltered. Collection by throwing-net to 8 feet depth. Associates: a sponge was collected. Algae, etc.: mainly diatoms; a few blue-greens; some filamentous Chlorophyceae; a few Chrysophyceae. Species collected: *Alona verrucosa*; one specimen only obtained.

Station III. Beach pools at head of Prapat Bay, 4 August 1953. Separated by sand and shingle beach from lake and nearby stream; probably filled from lake in storms; dried in dry weather; stony to sandy bottom. Associates: fauna

* I hope to show elsewhere that this species and *L. macrodonta* are local races of the same species, which thus comes to have a very wide distribution.

different from neighbouring part of lake; includes a *Limnaca*. Algae: filamentous diatoms; Chlorophyceae; and Cyanophyceae. Some *Nitzschia*. Species collected: nil.

TABLE I.—The Cladocera collected in L. Toba and the surrounding region by the Deutsche Limnologische Sunda-Expedition (as reported by Brehm, 1933), and during my visit to Prapat in August 1953.

SPECIES	MY COLLECTION		BREHM'S LISTS	
	In lake	In surrounding regions	In lake	In surrounding regions
<i>Diaphanosoma modigliani</i> Richard	+	—	+	—
<i>Diaphanosoma sarsi</i> Richard	—	—	+	—
<i>Latonopsis australis</i>	—	—	+	—
<i>Simocephalus vetulus</i> (O. F. Miller)	—	+	—	—
<i>Simocephalus exspinosus</i> (Koch)	—	+	—	—
<i>Simocephalus serrulatus</i> (Koch)	—	—	—	+
<i>Scapholeberis kingi</i>	—	—	—	+
<i>Ceriodaphnia dubia</i> Richard	+	—	+	—
<i>Ceriodaphnia cornuta</i> Sars	—	+	—	—
<i>Bosmina</i> sp.	—	—	+	—
<i>Macrothrix sumatrensis</i> (Brehm)	—	—	+	+
<i>Macrothrix triserialis</i> Brady	—	+	—	—
<i>Macrothrix spinosa</i> King	—	+	—	—
<i>Macrothrix tobaensis</i> , sp. nov.	+	—	?	—
<i>Ilyocryptus halyi</i> Brady	+	+	+	—
<i>Leydigia leydigi</i> (Schödler)	—	+	—	—
<i>Euryalona orientalis</i>	—	—	—	+
<i>Alona glabra</i> Sars	—	?	—	+
<i>Alona ? intermedia</i> Sars	+	—	—	—
<i>Alona verrucosa</i> Sars	+	+	—	—
<i>Alona</i> cf. <i>cambouei</i>	—	—	—	+
<i>Alona archeroides</i> Brehm	—	—	—	+
<i>Alona davidi</i> Richard	—	+	—	—
<i>Alona karua</i>	—	—	—	+
<i>Alonella excisa</i>	—	—	—	+
<i>Chydorus barroisi</i> Richard	—	+	+	+
<i>Chydorus robustus</i> Stingelin	—	—	+	—
<i>Chydorus</i> cf. <i>ventricosus</i>	—	—	—	+
<i>Chydorus sphaericus</i> Sars cf. <i>leonardi</i>	+	—	—	—
<i>Chydorus sphaericus</i> Sars forma	—	+	—	—
<i>Pleuroxus aduncus</i> var. <i>laticaudatus</i> Brehm	—	—	+	—
TOTALS	7	12	10	11

Station IV. North Hotel Bay, Prapat Peninsula, 15 August 1953. Moderately exposed; at the time of collection the water was undisturbed, subsequent to two days of on-shore winds. Plankton to depth over 4 feet. Bottom mainly rocks; partly sand. Associates: *Cyclops* and *Diaptomus*. Algae, etc: *Microcystis*, *Botryococcus* and floating debris. Species collected: *Ceriodaphnia dubia*; scarce. Both the typical form and the form with spinous fornice were present.

Station V. Cape near Boat-dock, Prapat Peninsula, 6 August 1953. Exposed; rocky. Throwing-net used for plankton. Associates: *Diaptomus* sp.—not very numerous. Algae: *Coelosphaerium*, *Microcystis* and *Botryococcus* were dominant. Species collected: *Ceriodaphnia dubia*. Very scarce. Form with spinous fornice.

Station VI. Public bathing-beach, Prapat Peninsula, 19 August 1953. Not very exposed; bottom mainly sandy with occasional rocks and *Myriophyllum*. Tow-netting to circa 4 feet depth. Associates: *Diaptomus* abundant; small *Eucyclops* scarce; Caenid nymphs. Algae, etc.: *Botryococcus*, *Microcystis*, *Volvox*, etc. None really abundant. Species collected: *Diaphanosoma modigliani*—two specimens only obtained. Both damaged in collection. *Ceriodaphnia dubia*—very scarce; both forms were present; eggs nil; guts empty.

Station VII. Beach pools at head of Prapat Bay, 25 August 1953. Pools almost vanished. Species collected: nil.

Station VIII. Pasang Grahman Bay, Prapat Peninsula, 4 August 1953. Fairly sheltered; detritus abundant. Associates: a still-water 'Insectan' fauna with many small fish. Algae, etc.: very sparse save for epiphytic diatoms and some very small flagellates. Species collected: *Alona verrucosa*, non-verrucose form: a single individual.

Station IX. South Hotel Bay, Prapat Peninsula, 5 August 1953. A very sheltered, very small bay, projected by a jetty; bottom of very fine sand to silt. Vegetation (*Nymphaea*; *Myriophyllum*, *Potamogeton*, etc.) abundant. Associates: a rich still-water fauna including many insect larvae, *Limnaea* sp., copepods and ostracods. Algae: many epiphytes including Cyanophyceae and diatoms; some *Bulbochaete* and *Oedogonium*; other algae (small *Trachelomonas*; *Coelosphaerium*; *Botryococcus*, etc.) not very abundant. Species collected: 5 August 1953: *Macrothrix tobaensis*—scarce, *Ilyocryptus halyi*—scarce, *Chydorus sphaericus* cf. *leonardi*—scarce; 17 August 1953: *Chydorus sphaericus* cf. *leonardi*—scarce.

Station X. Sipiak Bay, 20 August 1953. Sheltered, but much disturbed by ferry-boats; depth *circa* 1 foot: sandy, no vegetation. Tow between jetties in calm weather. Algae, etc.: scarce, similar to Station VI but *Glenodinium* present in addition. Species collected: nil.

Station XI. Washplace, South Bay, Prapat, 25 August 1953. Fairly sheltered: bottom very fine sand to silt. Vegetation (? *Potamogeton*; *Myriophyllum*, etc.) abundant. Associates: fairly rich still-water fauna with some Ostracods and Copepods. Algae, etc.: epiphytic blue-green algae and diatoms abundant; some *Bulbochaete* and *Oedogonium*; other algae (small *Trachelomonas*; *Coelosphaerium*; *Botryococcus*, etc.) not very abundant. Species collected: *Chydorus sphaericus* cf. *leonardi*—very scarce.

Station XII. South Bay, Prapat, between water-hyacinths at bay head, 8 August 1953. Very fine mud-bottom; very sheltered: disturbed by boats, etc. Associates: Atyid prawns; young fish. Species collected: *Chydorus* sp. one individual; very deeply pigmented; ocellus invisible.

Station XIII. Open lake opposite mouth of Prapat Bay, 10 August 1953. Surface tow-netting. Zooplankton very scarce; a few *Diaptomus* copepodids. Species collected: *Ceriodaphnia dubia*, one large individual, with ordinary fornices; two eggs.

Station XIV. Artificial pond: Prapat Peninsula, 7 August 1953. Hand-net collection. Small artificial pond. Some *Myriophyllum*. Water somewhat greenish in colour, indicating rich nannoplankton. Associates: Ostracods; *Brachionus*. Bottom algae, etc. Bottom algae very abundant in large flocculent masses: *Pediastrum*, two spp.; *Scenedesmus* spp.; *Coelastrum* sp.; palmelloids; small green unicells; *Oedogonium*; *Mougeotia*; *Euastrum* sp. *Botryococcus fusca*; *Aulosira*; *Glenodinium* sp., etc. On 24 August 1953, it had dried up. Species collected: *Alona* ? *glabra*, one cast carapace. *Alona verrucosa*—only two specimens obtained, probably owing to difficulty of separation amongst the algal masses. Guts packed with green algae, size up to diameter of gut.

Station XV. Pool near Resthouse, Prapat Peninsula, 21 August 1953. One to two yards from edge of lake. ? Receives water from this at times of storm. Very small pond, *circa* half to two inches deep at time of collecting, in what was probably a deserted padi seed plot; very muddy. Associates: tadpoles and ostracods abundant; caenid nymphs numerous. Algae, etc.: detritus abundant; algae moderately abundant, of small-pool type, but with a rather high percentage of desmids, and also *Chroococcus* and *Aphanocapsa*. Species collected: *Ilyocryptus halyi*—numerous. Eggs nil.

Station XVI. Marshes in South Bay. Collections in typical marsh-pools surrounded on three sides by marsh vegetation, and on the fourth merging into

somewhat polluted water-meadows. The marshes form a continuous but narrow belt between fallow padi and the lake.

Station XVIa. Marsh-pool 1, 8 August 1953. Small and shallow; muddy bottom. Associates: rich, small-pond fauna. Algae, etc.: *Spirogyra* spp. abundant; euglenoids moderately abundant; diatoms scarce. Much detritus. Species collected: *Simocephalus exspinosus*—very scarce; four eggs; guts packed mainly with detritus but with some small green algae. *Macrothrix triserialis*—very scarce; egg-number apparently low.

Station XVIb. Marsh-pool 2, 8 August 1953. Deeper than pool 1; More clear water. *Utricularia* spp. present. Otherwise similar. Washings from *Utricularia* yielded some Copepods and many Ostracods. Species collected: *Simocephalus vetulus*—one male. Guts packed with detritus; a very little algae; and some free chlorophyll. *Veridaphnia cornuta*—hornless, setose form; two eggs; gut packed with detritus. *Macrothrix triserialis*—one specimen only; three eggs. *Ilyocryptus halyi*—one young. *Alona davidi*—one individual in washings from *Utricularia*. This pool had dried up on 24 August.

Station XVIc. Marsh-pool 3, 24 August 1953. Deeper into marshes and a deeper pool than 1 and 2. Associates: rich pond fauna. Algae, etc.: much detritus; algae rather sparse; generally of small-pond type but with *Tetradron* spp. and two sp. of *Cosmarium*. Species collected: *Simocephalus exspinosus*—scarce; eggs of two large individuals 10 and 14; guts packed with remains of small green algae. *Macrothrix spinosa*—very numerous; egg-number 1, 9 and 6; guts mainly filled with detritus. *Chydorus barroisi*—scarce. *Chydorus sphaericus* fma.—scarce.

Station XVII. Pools in fallow padi, South Bay, 24 August 1953. Probably almost permanent drainage 'tract' and adjoining pools four to six inches deep. Very muddy, little vegetation. Hand-net collection. Associates: Chironomids; Corixids; mosquito larvae; small Naiid Oligochaetes. Algae, etc.: detritus abundant. Much *Spirogyra*; some *Oscillatoria*; many minute flagellates especially colourless ones. Other algae scarce. Species collected; *Macrothrix spinosa*—very numerous; eggs $7 \pm .33$; feeding on detritus. *Ilyocryptus halyi*—abundant; egg-number apparently high. *Leydigia leydigi*—scarce; resting eggs.

Station XVII. Slow streams on Samosir, 10 August 1953. These were sluggish portions of streams very near their outflow into the main lake, flowing between padi-fields. They were very highly polluted and had some higher plants and large flocculent masses of floating algae and detritus. Species collected: nil.

NOTES ON THE SPECIES.

Diaphanosoma modiglianii Richard.

Two specimens of this species were obtained from Station VI. They were somewhat damaged in collection and preserved badly. However, the post-abdomen agreed with this species, and since, according to both Richard (1895) and Brehm (1933), it is the more common of the two species of this genus which occur in the lake, the identification seems certain.

Simocephalus.

All of the three cosmopolitan species of this genus have been previously recorded from Sumatra, though *S. serrulatus* (Koch) was the only species found by the Deutsche Limnologische Sunda-Expedition. The only other species likely to occur here is *S. acutirostratus* (King). In 1933 Brehm tentatively synonymized this species with *S. exspinosus* (Koch). Misled by this I described (Johnson, 1953) a new species, *S. acutifrons*, from South Africa. Having subsequently seen Sars' (1895) description of *S. acutirostratus*, I am now convinced that *S. acutifrons* is at most a local race of *S. acutirostratus*. This species has also been recorded from Brazil (Brehm, 1937), so that it is very probable that it has a pan-tropical distribution, and will thus be eventually found in the Sunda Archipelago.

In my collections at Prapat I collected both *S. vetulus* (O. F. Müller) and *S. exspinosus*. None of the pools in which I collected was highly acid and this probably explains in part my failure to find *S. serrulatus*.

Simocephalus vetulus (O. F. Müller).

A single male of this species was collected from the marsh-pool at Station XVIIb. In general features it corresponded to the variety *productifer* which is the only form of this species recorded from Sumatra (Brehm, 1933).

Simocephalus exspinosus (Koch).

This species occurred in the marshes of the South Bay at Stations XVIa and XVIIb. The egg-numbers of the two individuals examined from the latter station were 10 and 16, indicating favourable conditions.

Both populations consisted of individuals of typical form and pale coloration. The cross-bars between the carapace striations were rather numerous, giving rise to a brick-like appearance in places.

Ceriodaphnia cornuta Sars = *Ceriodaphnia rigaudi* Richard.

A single specimen of the hornless variety of this species was collected from Station XVIIb.

It has been generally considered that *C. rigaudi* Richard is only a hornless form of *C. cornuta* Sars. However, Jenkin in 1934 declared that two species could be distinguished, each having horned and hornless forms, one species being *C. cornuta* Sars and the other *C. rigaudi* Richards. Harding (1942), on the basis of some intermediate specimens, decided that the distinctions drawn by Jenkin were untenable. I agree with his opinion. My specimen agreed with the hornless form of *C. rigaudi* Richard, Jenkin, but had the post-abdomen somewhat tapering—approaching *C. cornuta* Sars, Jenkin.

Dorsally the carapace bore numerous, long, fine hairs. Such specimens have previously only been recorded from East Africa (Jenkin, 1934).

Ceriodaphnia dubia Richard.

Lake Toba is the type locality of this widespread though poorly understood species. The species has been recorded from almost the whole world, but under a wide variety of names. One of the many forms which is almost certainly synonymous with it is the European *C. affinis* Lilljeborg.

I am very familiar with this latter species, which I have used as an experimental animal, and I have been unable to detect any significant differences between it and my specimens from Lake Toba. It may be noted here that the form and armature of the post-abdomen, the general body and head form, and the carapace markings of the two 'species' correspond exactly.

Richard (1895) does not mention the very fine weak comb of many teeth which occurs on the claws of *C. affinis* and is usually taken as diagnostic for the species. Brehm (1933) adds nothing to Richard's description. It is therefore important to note that the ciliation of the claws of my specimens is exactly comparable to that found in European specimens. Thus the last possible distinction between the two species is removed.

It may be noted that one feature often used to distinguish this species from the closely allied *C. pulchella* is not valid. *C. dubia* is commonly described as lacking a post-ocular bulge. In fact such a bulge is always present, though normally smaller and flatter than in *C. pulchella*.

Brehm, in discussing the form from Lake Toba, remarks, "Als ich die Toba-Meer-Proben untersuchte und nicht daran dachte, dass Richard von hier die *Ceriodaphnia dubia* beschrieben hat, glaubte ich entweder *C. quadrangula* oder *pulchella* vor mir zu haben". This is sufficient indication of the similarity of the three species since Brehm at this period was certainly more of a 'splitter' than of a 'lumper'.

TABLE II.—A comparison of four species of *Ceriodaphnia*.

Species	Post-ocular bulge	Dorsal margin of post-abdomen	Accessory spines internal to main series of anal spines	Combs on claws	Position of lateral seta on antennule
<i>C. quadrangula</i> .	None.	Concave proximal to anus.	None.	None.	?
<i>C. pulchella</i> .	Always present. Usually very well marked.	Straight or convex proximal to anus.	Present.	None.	Inserted at 9/10 length from antennule base.
<i>C. dubia</i> .	Always present. Slightly to moderately well developed.	Straight or convex proximal to anus.	None.	A weak comb of very numerous, very fine teeth, only a little stronger than the general ciliation.	Inserted at or about 2/3 length from antennule base.
<i>C. rectangularis</i> .	Present or absent. At most very slight.	Straight or convex proximal to anus.	None.	A powerful comb of a very few, very stout teeth.	Inserted sub-terminally on a long protuberance.

Nevertheless I feel that the three species are readily separable, as is shown in Table II. I have included *C. reticulata* in this table, since Stingelin (1914) considered this species to be synonymous with *C. dubia*, though, as was pointed out by Gurney (1927), this opinion is clearly untenable.

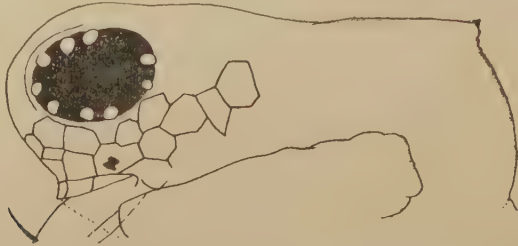


FIG. 2.—*Ceriodaphnia dubia*. Head of female of form with spinous fornice, from Prapat, August 1953. Magnification $\times 200$.

C. dubia var. (Fig. 2.)

About half of the individuals which I collected, mainly young ones, showed slight divergences from the typical form. These did not differ in any features which are not known to be variable in this group, so that I am only describing them as an unnamed variety. The differences from the typical form are: (a) the post-ocular protuberance is only very slightly developed; (b) the fornice are angular and bear one or a few very short spines; and (c) the carapace reticulation is much more clearly defined. The antennule, and the shape and armature of the post-abdomen, are as in the typical form. This variation parallels similar limnetic varieties found in *C. quadrangula*, *C. pulchella*, and *C. reticulata*.

Macrothrix.

Three species of this genus are known to occur in South-east Asia: *M. sumatrensis* (Brehm) (= *Gurneyella sumatrensis* Brehm), *M. triserialis* Brady, and *M. spinosa* (King). All three species have been collected in Sumatra but only *M. sumatrensis* is recorded from the Toba region. By contrast I failed to find *M. sumatrensis*, but obtained specimens of both the other species, and also of a third form showing some resemblance to *M. spinosa* and also to the Australian *M. hystrix* Gurney, but which cannot be identified with either, so that I am describing it as new (page 81).

Macrothrix triserialis Brady = *M. chevreuxi* Richard.

This species was found in the marshes in the South Bay at Stations XVIa and XVlb. It is a very common species in small pools in South-east Asia where it appears to fill the ecological role occupied by *M. laticornis* in Europe. In life it bears a strong resemblance to the latter species in size, general appearance, and behaviour. Jenkin (1934) has attempted to distinguish *M. chevreuxi* from *M. triserialis* by the following features of the former: (a) the presence of transverse irregularly anastomosing lines of sculpturing on the carapace; (b) the greater length of the antennules which are of almost equal length throughout and carry unequal olfactory setae; (c) the rather less heavily armed post-abdomen and the rather more spiny claws; and (d) the form of the labrum. In these features, with the exception of the claws, my specimens agree with *M. chevreuxi*. However, they should on geographical grounds belong to *M. triserialis*, which is the South-east Asian species. *M. chevreuxi* is described from S. America and Africa. Jenkin admits that *M. triserialis* is not very clearly defined, and to me it seems probable that the apparent differences between the two species are due to the inadequate descriptions of *M. triserialis*. There is no evidence that two forms occur in South-eastern Asia, and unless such evidence is forthcoming it is safer to revert to the old

view that *M. triserialis* and *M. chevreuxi* are the same species and amend the definition of *M. triserialis* accordingly. Thus *M. triserialis* will be established as one of the pan-tropical Cladocera.

Macrothrix spinosa (King).

Brehm (1933) remarks in discussing the distribution of this species that it appears to have a more restricted range than *M. triserialis*. Whilst this may be so it seems more probable that it has been commonly overlooked. It is a species which appears to be confined to very small water-bodies, and is itself of very small size, so that it could easily escape observation. In my collections at Prapat it occurred at Stations XVIc and XVIII.

There has in the past been considerable confusion concerning this species, and certainly some of the forms referred to it do not belong here. Nevertheless, there is a well-defined central group of forms to which most of the individuals collected in South-east Asia can be assigned. I am separating as a new species some individuals which differ considerably from this group (page 81) in this paper. Brehm gives a long discussion of those forms that have been assigned to the species, and no useful purpose would be served by repeating this here. It suffices to point out the important distinguishing features of the species as found in Malaysia. These are: (a) the small size (0.6 mm.); (b) the characteristic antennule, which is distinctly broadened towards the tip; (c) the dorsal margin of the carapace, which is crossed by parallel transverse ridges which may give the appearance of dorsal serration but are usually not sufficiently well developed to cause this; (d) the characteristic carapace sculpture which is an irregular reticulation, and which, at least in the centre of the carapace valves, appears squamous, is only moderately well developed, and may be scarcely visible in mounted specimens though always distinctive in the living animal; (e) the ventral margins of the carapace valves, which are toothed and bear the usual long setae; (f) the comparatively small ocellus; (g) the form of the short blunt rostrum; (h) the form and armature of the more or less distinctly bilobed post-abdomen; and (i) the large nuchal organ.

My specimens agree in all respects with this diagnosis. In addition I was not able to find groups of spines on the antennae (such as occur in *M. hystrix*), and all the antennal setae of my specimens bore longitudinal rows of spinules. In the specimens from Station XVII, I was able to detect a faint vermiculation on the anterior region of the head, but this was apparently absent from the specimens obtained from Station XVIc.

Macrothrix tobaensis, sp. nov. (Fig. 3.)

From Station IX, I obtained several specimens of a *Macrothrix* which closely resembles *M. spinosa*, but differs too much to be included therein. Unfortunately, only one specimen is sufficiently well preserved for description. Normally I would hesitate to establish a new species in this difficult group on the basis of a single good specimen. However, Brehm (1933) records an unnamed form from an undetermined locality in the greater Sunda Islands, which he assigns to *M. spinosa*, and which appears from his rather short description to be the same as my form. Thus I can be fairly confident that I am not dealing with an aberrant individual, an impression confirmed by my field notes of my other specimens.

The type is a parthenogenetic female from Station IX, Prapat, Lake Toba, North Sumatra. It is mounted on a slide in Euparal and will be deposited in the British Museum (Natural History), London.

The species is a small *Macrothrix* closely resembling and obviously nearly allied to *M. spinosa* and *M. hystrix*. The general contour of the head and carapace is as in *M. spinosa*, but the rostrum is somewhat longer than is usual in that species and in life there is a distinct small embayment in front of the ocellus. The rostrum, though somewhat shorter and less well defined, thus closely resembles that of *M. hystrix*.

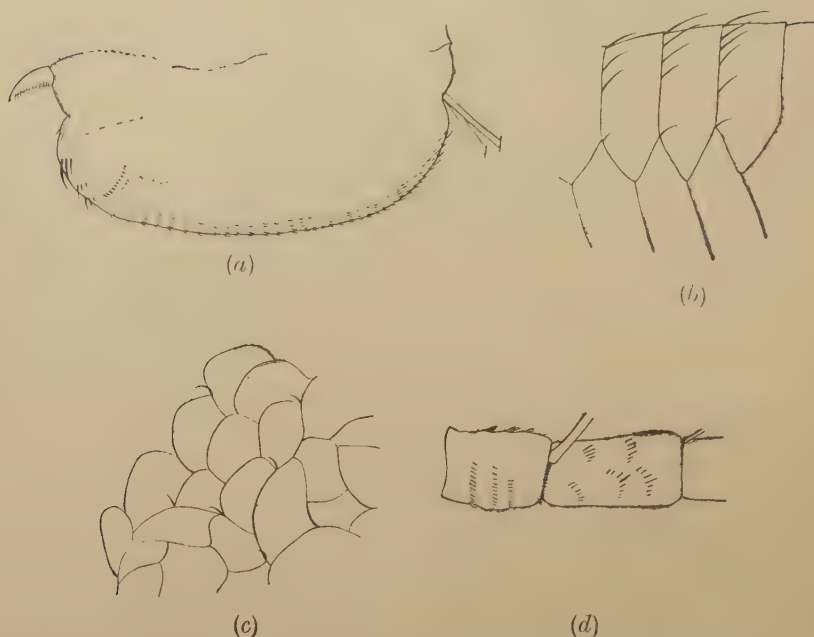


FIG. 3.—*Macrothrix tobaensis*, female, from Prapat, August 1953.

- (a) Post-abdomen. Magnification $\times 250$.
 (b) Sculpture of dorsal region of head. Magnification $\times 250$.
 (c) Sculpture of a portion of a carapace valve. Magnification $\times 250$.
 (d) Portion of ventral ramus of antenna. Magnification $\times 250$.

The carapace is marked by an exceedingly conspicuous squamous sculpturing, which has a regular transverse arrangement on the dorsum. The sculpturing is sufficiently pronounced to cause a definite though minute serration of the dorsal margin, corresponding to the raised sculpture-lines. This squamous sculpturing occurs also on the labrum and even extends unto the abdomen. The head and carapace are setose dorsally, though much less so than in *M. hystrix*. The setae are very conspicuous in life and in an aqueous medium, but are not very easy to observe in a mounted specimen. They are short, stiff, and curved, as in *M. hystrix*. On the head they tend to be arranged in transverse rows; but on the carapace they are much less numerous, confined to the dorsal region and arise singly from some of the nodes of the carapace reticulations. The rows of setae on the head are also associated with the sculpture-lines. On the dorsal margin of the carapace they are replaced by stouter, shorter, and blunter spinules.

The nuchal organ is small and notch-like. The eye is large; the ocellus rather small. The antennules are broadened at the tip and closely resemble that shown in Gurney's figure 6A of *M. hystrix*, though showing little resemblance to his figure 6B (Gurney, 1927). They differ in being more rounded at the tip, and in having the postero-distal cluster of spines placed nearer to the tip. The olfactory setae are unequal. As far as I can determine they consist of two subequal long setae, two slightly shorter setae and the remainder, which are conspicuously shorter. The antennae bear numerous more or less transverse rows of spinules, resembling those shown by Gurney for *M. hystrix*. All the antennal setae bear longitudinal rows of spinules as in *M. spinosa*.

The post-abdomen is not bilobed and shows no trace of this condition. In form and in general spinulation it is very similar to that of *M. hystrix*.

The species is distinguished from *M. spinosa* by the form and spinulation of the post-abdomen; the small nuchal organ; the slight embayment in front of the ocellus; the rows of spinules on the antennal segments; the much more conspicuous carapace sculpture; and the presence of numerous short setae on the dorsal region of head and carapace. Experience in other Cladoceran genera suggests that the latter feature may not be constant. It is distinguished from *M. hystrix*, which it resembles in most of the above features, by the presence of teeth on the ventral carapace valves; by the presence of squamous sculpturing on the carapace valves; by the longitudinal rows of spinules on the setae of the antennae; by the minute serrations on the dorsal margin of the carapace; by the shorter rostrum; by the absence of a notch between head and carapace; and by the much more sparse, much less regularly arranged setation of the head and carapace.

Ilyocryptus halyi Brady.

This appears to be one of the commonest species of Cladocera in the area. I collected it at Stations IX, XV, XVIb, XVIII. Brehm (1933) comments that Spandl figures five long lateral bristles on the distal region of the post-abdomen, whereas he always finds six such bristles in his material. A sample of ten individuals from Station XVII contained seven with six bristles and three with seven bristles.

Leydigia leydigi (Schödler).

A single specimen of this species was obtained from Station XVII. Hitherto this species has usually been considered to be confined to the palaearctic region. The closely allied *L. macrodonta* Sars is an African form. Neither has been previously recorded from the Malaysian region. I hope to show elsewhere that *L. leydigi* and *L. macrodonta* are no more than geographical races of the same species. The present specimen confirms this conclusion. Jenkin (1934) described a *Leydigia* from East Africa which was in some respects intermediate between *L. leydigi* and *L. macrodonta* and which she describes as *L. macrodonta* var. *louisii*. My specimen most closely resembles this form but differs in several important respects. Unlike Jenkin's form and *L. macrodonta* s.s., but agreeing with *L. leydigi*, the ocellus of my specimen is square. The specimen agrees with *L. macrodonta* s.s. in having perfectly smooth carapace valves, in contrast to the granulated carapace valves found in *L. macrodonta* var. *louisii* and, at least commonly, in *L. leydigi*. The form and armature of the post-abdomen is almost exactly as in *L. macrodonta* var. *louisii* but the groups of long lateral spines do not show a division into two inner long and two outer short spines. Rather they decrease regularly in size towards the outer ends of each row. Each row contains four or five spines. The claws are very strongly ciliated; but I was unable to detect the 'alonopsiform' type of ciliation which Jenkin describes for *L. macrodonta* var. *louisii* and which, as she remarks, sometimes occurs in *L. leydigi*. The basal spine of the claws is rudimentary as in *L. macrodonta* s.s., being very much smaller than in typical *L. leydigi* or in *L. macrodonta* var. *louisii*. In other features my specimen does not differ essentially from Jenkin's form. The distribution of characters between these four forms strongly suggests the typical pattern of a polytypic species split up into subspecies. Since I have only one specimen of the Sumatran form I prefer not to name it, since it is impossible to tell how far the differences it shows from the other forms are due to individual variation.

Alona.

The genus *Alona* and the closely allied genus *Alonella* are in a state of utter chaos, and sadly in need of a thorough revision. Brehm (1933) provided a synopsis of the species known to him and a key to both genera. Unfortunately he accepted the traditional boundaries between the two genera, making no attempt to deal with the problem raised by the species which Birge (1918) includes in the subgenus *Paralonella*. In addition, Brehm's synopsis of the characters of the described species of *Alona* is very brief and in some places distinctly misleading; whilst his key is

incomplete and somewhat inaccurate. Later comments by Jenkin (1934) and Brehm (1937) have helped to remove some obscurities but have not really dealt with the root-problem of the classification of this group of genera.

In delimiting the genera I have included the *Paralonella* group in *Alona*. Whilst I am conscious that this is unsatisfactory, it seems to be less so than the two other courses available at the present moment. *Alona* is in any case a large and heterogeneous genus, whilst *Alonella* becomes a natural or nearly natural unit when the *Paralonella* group is removed from it. The course of erecting a new genus to include these forms is not advisable in the absence of a thorough revision.

The chaotic state of the genus and the inadequate nature of many specific descriptions inevitably result in a certain amount of uncertainty in some of the specific determinations. Where my forms differ slightly from previously described species I have assigned them, sometimes with a ?, to these species, since I am convinced that the creation of new species in this genus serves no useful purpose unless they are very distinct from previously described species. It is almost certain that when the genus is thoroughly revised many of the existing species will be merged and there is no gain in creating new species, which would almost certainly suffer the same fate.



FIG. 4.—*Alona?* *glabra* from Prapat, Station XIV, August 1953. Post-abdomen. Magnification $\times 200$.

Alona? *glabra* Sars. (Fig. 4.)

A single exuvium obtained from Station XIV appeared, from the general form of the carapace, the absence of longitudinal striations, and the form and armature of the post-abdomen, to come closest to this species. The species also showed some resemblance to *A. arenaria* Brehm which was described from Bali. Brehm (1937) later synonymized *A. arenaria* with *A. pulchella* King, but it is by no means established that this synonymy is valid. In the same paper he also suggests that *A. glabra* is also a synonym of *A. pulchella*. I prefer not to give judgement on this question but note that, as Brehm remarks, the post-abdomen of *A. glabra* is shorter than in typical *A. pulchella* and *A. arenaria*. Hence it is relatively broader. Furthermore *A. glabra* is distinguished by the arrangement of the anal denticles, which are rather long and slender and have the distal three somewhat enlarged. In all these features my specimens agree with *A. glabra* rather than with *A. arenaria*. I was not able to detect any striation of the carapace valves, nor was the distal corner of the post-abdomen rounded off, so that a reference to *A. pulchella* s.s. is out of the question. Whilst I agree that it is possible that all these species will ultimately prove to be synonymous, I have thought it better to be over-precise in my determinations rather than assign the form to the vague and ill-defined grouping of *A. pulchella* s. lat.

Alona? *intermedia* Sars.

A single specimen from Station I is assigned to this species on the basis of the form and armature of the post-abdomen, which is slightly expanded distally and bears strong fascicles which over-lap the margin; and the untoothed labrum. The species is not very clearly defined and possibly includes more than one species. In form of post-abdomen the individuals assigned here by some authors (e.g. Scourfield & Harding, 1941; Gurney, 1927) seem to be scarcely different from *A. verrucosa*. On

the other hand, the forms figured by Sars (1916) and Lilljeborg (1900) have a post-abdomen which vaguely recalls the *quadrangularis* group, though also similar in some ways to that of *A. rectangula*. My specimen is of this latter type, which I take to be the typical form for the species, except that the pre-anal portion is long as in *A. rectangula* and *A. verrucosa*. In the presence of longitudinal striae and the lack of punctations my specimen again approaches *A. intermedia*, but the striations are very faint indeed, being invisible when the specimen is mounted in Euparal, an unusual condition for *A. intermedia*. Jenkin's ratios (see Jenkin, 1934) for this individual are L. 43, W. 44, D. 28. Whilst the general appearance of the post-abdomen recalls the true *A. intermedia* of Sars, in these ratios it comes closest to the form figured by Scourfield and Harding and to *A. verrucosa*. Ratios for *A. verrucosa* are given below under that species. For purposes of comparison I shall give here the ratios for the two types of *intermedia*. These are, for Sars' form, L. 30, W. 37, and D. 22, according to Sars' figure (Sars, 1916), and L. 26, W. 42, and D. 22 from Lilljeborg's figure. For the form of Scourfield and Harding I obtain the ratios L. 44, W. 43, and D. 24. Unfortunately it is not as yet possible to assess the value of such ratios as discriminating characters. Certainly they are not so reliable as Jenkin supposed. In the circumstances I can only assign my specimen to *A. intermedia* with some doubt.

Alona verrucosa Sars, Jenkin. (Figs. 5 and 6.)

? = *A. verrucosa* Lutz, 1878.

= *A. verrucosa* Sars, 1901; Jenkin, 1934; Brehm, 1937.

= *A. verrucosa* Sars var. Stingelin, 1904.

? = *A. anodonta* Daday, 1905.

= *A. alonopsiformis* Brehm, 1933 b.

A single individual of this species was obtained from each of Stations II and VIII and two individuals were obtained from Station XIV. The species was probably not uncommon in the latter habitat in which the accumulation of algae and detritus was such that it was exceedingly difficult to search for and detect small Cladocera. The specimens differed somewhat amongst themselves and from Jenkin's excellent descriptions and so merit a rather extensive discussion. All however can be assigned to this species without any doubt.

The specimen from Station VIII agreed with Stingelin's variety in lacking all trace of the 'verrucae' which give the species its name (fig. 5a); otherwise, however, the carapace markings were fully typical. It may be noted that the characteristic wavy faint longitudinal striae were present. Jenkin suggested that the waviness was the result of the irregular surface of the carapace. Its presence in this specimen which lacks these irregularities, suggests that it is a useful independent character. The labrum bore the characteristic tooth on the anterior margin. The post-abdomen (fig. 6a) differed in details of its armature from the type figured by Jenkin. Proximal to the principal anal denticles there was a continuous row of small denticles instead of the groups of denticles which Jenkin figured. The fascicles were exceptionally long and I was only able to detect a single very stout bristle in each, though some of these bristles showed signs of having arisen by fusion of two or more rudiments. A very similar appearance is sometimes given by the fascicles of *Alona intermedia*, as is well known. Moreover, Brehm (1937) has drawn attention to a similar reduction in the numbers of bristles in the lateral fascicles found in members of *A. pulchella* s. lat. The fine bristles of these lateral fascicles are, in addition, often very difficult to observe, and I cannot be absolutely certain that very fine accessory bristles were not present, though certain that they could not be observed with a 1/12 inch oil-immersion objective. This difference in setation is thus of considerably less importance than appears at first sight. The claw shows the vaguely 'alonopsiform' ciliation characteristic of this species. The ratios of the post-abdomen will be given below.



FIG. 5.—*Alona verrucosa* from Prapat, August 1953.

- (a) Individual with depressions from Station VIII. Magnification $\times 80$.
 (b) Individual with depressions on the antero-dorsal region, and with forwardly directed labrum, from Station XIV. Magnification $\times 80$.
 (c) Head of this individual. Magnification $\times 200$.

The specimens from Station XIV both showed the '*verrucosa*' carapace structure in a well-developed form. In one specimen this structure covered the whole carapace, completely obscuring the normal striation and punctation; but in the other specimen it was only conspicuous on the head and the dorsal portion of the carapace (fig. 5*b* and *c*). In these specimens the form and armature of the post-abdomen (fig. 6*b*) agreed very closely with that of the specimen figured by Jenkin. The fascicles were of typical form and the row of fascicles extended on to the pre-anal region. The groups of spines proximal to the principal marginal denticles were much as in Jenkin's form. There were 11 principal marginal denticles and lateral fascicles. The post-ventral corner of the carapace had the typical *verrucosa* structure. In one specimen the tooth on the labrum was clearly visible. In the other this was obscured, since the labrum was bent forwards—giving it a very aberrant appearance.

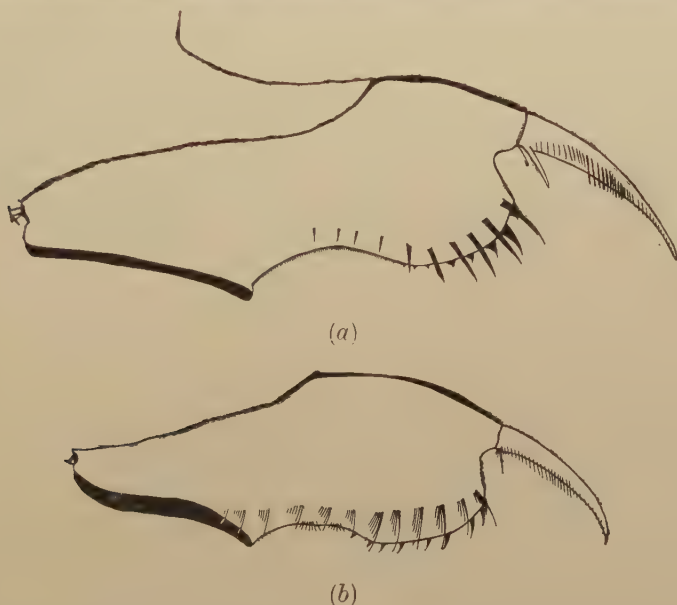


FIG. 6.—*Alona verrucosa* from Prapat, August 1953. Post-abdomen.

(a) Post-abdomen of individual figured in fig. 5*a*. Magnification $\times 200$.

(b) Post-abdomen of individual figured in fig. 5*b*. Magnification $\times 200$.

It has been customary in the past to speak of the carapace of this species as bearing warts or elevations. In these two specimens the irregularities were very close together and it was obvious that they were essentially depressions rather than elevations. Whether this is more generally true cannot be determined; but this seems possible, since the optical appearances of isolated depressions and isolated elevations are very similar when these are viewed under a high-power microscope.

The specimen from Station II was essentially similar to those from Station XIV but the lateral row of fascicles only extended to the middle of the anal emargination.

The post-abdomen of these specimens from Lake Toba was somewhat narrower than in Jenkin's forms L. 41–42, W. 38–40, D. 21–23, as compared with L. 39, W. 43, D. 24. Thus contrary to Jenkin's opinion the width of the post-abdomen does not distinguish this species from *A. novae-zealandiae* Sars, though the general form and the long pre-anal region appear to be valid distinctions.

A. verrucosa, though somewhat variable, appears to be a well-defined species which is not uncommon in South-east Asia. It is also known from East Africa and South America. Thus it has at least a pan-tropical distribution. Certain figures of carapace structure suggest that some European forms assigned to *A. rectangularis*

are really forms of *A. verrucosa*. An example of these is Lilljeborg's figure of *Alona rectangula* var. *pulchra* Matile, 1890 (Lilljeborg, 1900, pl. lxix, fig. 1). This specimen has the typical carapace form of *A. verrucosa*; the carapace markings certainly could represent the 'verrucosa' structure and the labrum, though very indistinctly figured, appears to have a tooth. The post-abdomen is poorly figured but could represent that of *A. verrucosa*. The name *pulchra* has priority over *verrucosa* but fortunately *Alona pulchra* Hellich, 1874, appears to be a different species, so that *Alona verrucosa* remains the valid name for this species.* In the absence of further evidence it must remain uncertain whether *Alona verrucosa* occurs in Europe, but such occurrence is a strong possibility.

Jenkin (1934) and Brehm (1937) have both enumerated characters which serve to distinguish this species, but their enumerations are supplementary to each other, and certain of the characters on which they lay stress seem to me to be of minor importance. For this reason I shall give a list of the most important distinguishing features, roughly in order of their importance. The species is characterized by: (a) the general carapace form and in particular the emarginate ventral carapace margin; (b) the characteristic post-abdomen which appears to be slightly broadened towards the end, though it is really not so broadened, and has a characteristic boldly rounded, and projecting, post-distal corner; (c) the very extensive row of very well-developed lateral fascicles, most of which overhang the dorsal edge of the post-abdomen; (d) the characteristic toothed labrum; (e) the characteristic wavy longitudinal striation and thick punctation of the carapace, which may or may not be supplemented or obscured by equally characteristic elevations or depressions; (f) the somewhat 'alonopsiform' ciliation of the claws, a character which Brehm stresses but which is not always well marked; and (g) the detailed ciliation of the post-ventral corner of the carapace, a character stressed by Jenkin, but which is unfortunately very difficult to observe.

Alona davidi Richard = *Alonella diaphana* Brehm, 1933 nec (King) Sars, 1889.

One specimen of this species was obtained from Station XVIIb in washings from *Utricularia* roots.

Most authors have treated it as a synonym of *A. diaphana* (King), but Jenkin (1934) has pointed out certain features by means of which it can be distinguished. These are the unstriped, granulate carapace; the ciliated claws; the presence of groups of hairs on the side of the post-abdomen; and the presence of a well-defined pre-anal angle. I could not certainly detect any ciliation on the claws (a difficult character to eliminate with certainty when mounted specimens are being examined) but in the other features my specimen is clearly to be assigned to *A. davidi*. Brehm's figure leaves no doubt that his specimens from Bali were really representatives of *Alona davidi* which thus appears to be widespread in the Archipelago.

My reasons for referring this species to *Alona* have already been dealt with in my discussion of that genus.

Chydorus barroisi Richard.

This species occurred at Station XVIc. The specimens were quite typical with five teeth on the labrum, and one or two teeth at the post-ventral carapace angle.

Chydorus sphaericus O. F. Müller.

I have assigned to this species populations occurring at Stations IX, XI, and XVIc. Workers on European faunas would automatically assign all of these to the present species, and there seems to me to be little or no point in trying to perpetuate

* *Alona verrucosa* Sars, 1901 is itself a junior homonym of *A. verrucosa* Lutz, 1878, a species which is inadequately described and may or may not be the same as Sars' form. Owing to the similar uncertainty attaching to *A. anodonta* Daday it is unwise to abandon *A. verrucosa* Sars in favour of *A. verrucosa* Lutz, since this procedure would inevitably lead to confusion. I have written to the International Commission to request that they suppress *A. verrucosa* Lutz, 1878 and place *A. verrucosa* Sars, 1901 on the official list of specific names.

unreal specific distinctions just because the material examined is of exotic origin. Specimens from Station IX and XI correspond to var. *leonardi*. The specimens from Station XVIc are not assignable to any previously described form known to me, though corresponding exactly to a form of this species which I have observed in England. This form is distinguished by its medium size; the dark brown colour of the carapace, which lacks any clear reticulations; the presence of lateral ciliation on the post-abdomen; and the presence of a *single* chitinous knob, which lacks bristles, at the anterior end of the inner ventral margin of the carapace.

ECOLOGICAL NOTES.

The detailed local distribution of the species which I collected, together with notes on the general characters of the stations and the associated algae, is given under 'Notes on Stations'. For completeness I have included those stations where no Cladocera were found, even though the collecting method was suitable for the discovery of members of this group.

The most striking feature of this list is the rarity of almost all the species found—especially in the lake itself. The general impression given by Brehm's account suggests that in his collections also the littoral Cladoceran fauna was poorly represented. This is not a completely exceptional feature. The literature indicates that it is not unusual for littoral Cladocera to be extremely rare in large tropical lakes, and a similar rarity characterizes certain non-tropical lakes, of tectonic origin and large size, as for instance Lake Baikal. This feature reaches its limit in Lake Tanganyika, where Cladocera are completely absent save at river mouths. Several attempts have been made to explain this absence on the basis of the physics and chemistry of the lake waters, but none has been very convincing. It seems to me that no satisfactory solution will be obtained until it is realized that the situation in Lake Tanganyika is merely an extreme case of a very general problem. At the present time the available data are insufficient to allow any conclusions on the problem as a whole. As far as the littoral Cladocera are concerned it may be noted that most of those species which occur in South-eastern Asia seem to be essentially adapted for life in very small water-bodies, so that conditions in such a large, comparatively little-evolved lake as Lake Toba are hardly likely to be favourable.

An important factor which certainly does restrict the Cladoceran fauna of the littoral region of Lake Toba is the comparative absence of really sheltered inshore areas with thick vegetation. The two most sheltered localities in which I collected were the small bay behind the jetty in South Hotel Bay (Station IX) and the shallow water amongst the water-hyacinths in the South Bay (Station XII). The latter was in many respects not a suitable habitat for Cladocera (oxygen shortage; presence of numerous young fish, etc.) but did produce one species. The former was the only habitat within the lake from which I obtained more than one littoral species. It was also the only habitat within the lake at which the two Macrothricids present were collected. Other occurrences of these two species and their near allies show that both demand a fine, more or less muddy bottom, conditions which are only possible in sheltered parts of the littoral zone. As is usual in similar habitats in Europe, true littoral Cladocera were absent from the most exposed stations. In Europe certain Chydorids as *Alonopsis elongata* and *Pleuroxus truncatus* are sometimes found in such habitats; but these species do not occur in South-eastern Asia and no local species seem to be adapted for such a role. Species found in the more moderately exposed stations were *Chydorus sphaericus*, *Alona verrucosa*, and *Alona* cf. *intermedia*. *Chydorus sphaericus* is perhaps the most adaptable of Cladocera, whilst species of the genus *Alona* are often to be found in similar situations in European lakes. Thus, making allowance for their sparsity and lack of variety, the littoral Cladocera of this lake show a similar local distribution to those of European lakes.

The records of planktonic Cladocera (*Diaphanosoma modigliani* and *Ceriodaphnia dubia*) collected at inshore stations are of interest. They were accompanied by planktonic Copepoda, some of which, such as a species of *Diaptomus*, were quite numerous. Both Stations IV and VI were devoid of a continuous vegetation zone, and both were comparatively sheltered, and with undisturbed water at the time of my collections. I have similarly found plankton species inshore at such places in large European lakes. These occurrences tend to disprove the littoral-avoidance theory of Wesenburg-Lund (1904-1908, 1926) which has won widespread acceptance. Since planktonic Cladocera can and do occur inshore, their usual absence from such situations must be explained by factors other than a definite avoidance of the littoral region. In this connection it may be noted that most if not all planktonic Cladocera are quite capable of living in very shallow water-bodies if other conditions are favourable. The usual absence of such Cladocera from the littoral of large lakes is most probably due to a combination of three factors; (a) the presence of vegetation in the more sheltered areas, which may really be avoided, and certainly favour competing non-planktonic species; (b) the usually disturbed condition of vegetation-free littoral areas which will result in the destruction of many individuals; and (c) the resultant effect of a combination of random horizontal movements and diurnal vertical movements on the part of the planktonic Cladocera. The net result of these movements must inevitably be that at any one time the Cladoceran population per square metre of the surface waters of the open lake is higher than that inshore, save in those places where the true littoral Cladocera are abundant.

A further factor influencing the occurrence of Cladocera in the littoral region of the lake is the abundance everywhere, except in the most exposed localities, of young fish. Many young fish feed voraciously on Cladocera, and so it is usual to find a partially exclusive relationship between the distribution of young fish and the distribution of Cladocera. This must reinforce the factors already mentioned in restricting the numbers of Cladocera present in the littoral region of the lake.

The ponds and marshes do not present any features of exceptional ecological interest. As already mentioned, their Cladoceran fauna does not differ greatly from that of other similar ponds in South-east Asia. The general faunas of the ponds also closely resembles that of similar habitats in Europe. This type of small weedy pool dominated by *Macrothrix* spp., or members of closely allied genera, is probably to be taken as the normal type of small pool in moderately rainy areas, where the calcium content of the water is not very high, and where there is little extraneous organic pollution. The artificial pond, Station XIV, is of an entirely different type, particularly in the total absence of amphibious vegetation and of an earth bottom. The abundance of bottom-algae is also characteristic and the presence of a population of small Chydorids feeding on these algae agrees with my experience of similar pools in western Europe. The pool is remarkable, for its type, in not yielding any species of *Ceriodaphnia* or *Daphnia*, since representatives of one or other of these genera are normally found in such habitats. Their absence may be due to the comparative newness of the pool and its isolation from similar habitats.

SUMMARY.

An account is given of the Cladocera collected at Prapat, Lake Toba, during a month spent there in the summer of 1953. The collections are compared with those made by the Deutsche Limnologische Sunda-Expedition. Notes are made on the systematics of the species collected, and the paper concludes with a general ecological note.

ACKNOWLEDGMENTS.

My thanks are due to Professor R. D. Purchon of this laboratory, Dr. J. P. Harding of the British Museum (Natural History), and my wife, Dr. A. Garrard, for reading and criticizing this paper. I have also to thank the Indonesian Consul-General in Singapore and his staff, the British Consul at Medan, and the Custom's

Authorities at Belawan-Deli, for their very necessary and willing assistance in facilitating my trip to Lake Toba. I was assisted in this trip by a grant towards travelling expenses made by the University of Malaya and wish to thank the Bursar of this University for his assistance with the financial problems of the excursion.

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JOURNEY TO NORTHERN ETHIOPIA (SIMIEN), 1952-3 : ARACHNIDA, OPILIONES. Von Professor Dr. C. Fr. ROEWER, Bremen. (Communicated by Dr. HUGH SCOTT, F.R.S., F.L.S.)

(With 1 text-figure.)

[Read 21 October 1954.]

Etliche wenige Opilioniden wurden mir von Herrn Dr. Hugh Scott, der sie gelegentlich seiner Expedition nach Abessinien sammelte, zur Identifizierung übergeben. Die einzige neue Form darunter gehört zu den Assamiidae, und ich erlaube mir, sie artlich nach ihm zu benennen. Auf seinen Wunsch schliessen wir hier eine Liste der bisher aus Abessinien und den unmittelbar benachbarten Gegenden bekannt gewordenen Opilioniden an.*

Subord. OPILIONES LANIATORES.

Fam. Assamiidae.

Subfam. ERECINAE.

SIMIENATUS, gen. nov.

Mit den Merkmalen der Erecinae: Tuber oculorum unbewehrt, sehr breit und quer-oval: 1. Area des Scutums mit sehr deutlicher, breiter Medianfurche; 1.-5. Area des Scutums und freie Tergite des Abdomens unbewehrt; 4. Coxa lateral ohne einen grösseren Einzeldorn. Palpenfemur medial-apical unbewehrt. Beine: Gliedzahl des 1.-4. Tarsus 5, mehr als 6 (variabel), 6, mehr als 6; 1. Distitarsus 2- und 2. Distitarsus 3-gliedrig.

Simienatus scotti, spec. nov. (Fig. 1, a-c.)

♂, ♀: Länge des Körpers 4,2; des 1.-4. Beines 6, 10, 7, 11 mm.

Die ganze Dorsalfläche des Körpers mit Tuber oculorum gleichmässig mit spitzenhaarigen, stumpfen, groben Buckelkörnchen regellos bestreut, die am Hinterrande der drei freien Tergite am grössten sind und hier fast dörnchenartig hervortreten; unterer Stirnrand des Carapax mit einem kurzen Medianzahn und lateral mit einem stärkeren, spitzen, sowie lateral davon mit je 2-3 stumpfen Zähnen (fig. 1); freie Sternite mit je zwei unregelmässigen Körnchen-Querreihen, Stigmensternit und Fläche der Coxen gleichmässig grob bekörnelt wie die Dorsalseite des Körpers, Stigmen durch 4:3 Kugelkörnchen verdeckt (fig. 1 b). Cheliceren kräftig entwickelt, besonders beim ♂, der längsovale Dorsalbuckel des 1. Gliedes dicht bekörnelt, das 2. (Scheren-) Glied glänzend glatt. Palpen: Trochanter ventral mit 1 Stachel, Femur dick, stark S-förmig gekrümmt, medial-apical unbewehrt, ventral (in der Basalhälfte) mit etwa 8-10 ungleich-langen Dörnchen, dorsal wie die im übrigen unbewehrte Patella regellos bekörnelt, Tibia und Tarsus dagegen dorsal glatt und ventral wie

* [Besides the new genus and species obtained in the high Simien district during my journey to Northern Ethiopia, 1952-3, records are included of examples of a widely distributed East African species (*Cristina armata* Roewer) both from Simien in the north and from Soddu (Walamo Province) in the south, the latter example having been collected during my journey to Southern Ethiopia in 1948-9. Moreover two species (*Harsadia spinosa* Roewer and *Djemia cooperi* Roewer), described in 1935, were based on specimens collected by Professor Omer-Cooper during our joint expedition in 1926. These are included below by Professor Roewer in his list, which is a complete enumeration to date of the Opiliones known from Ethiopia, Eritrea and Somaliland. —HUGH SCOTT.]

üblich bewehrt (fig 1 c). Beine. Trochanteren und Femora regellos bekörnt, Tibien schwächer bekörnt, 3. und 4. Femur leicht S-förmig gekrümmt; Zahl der Tarsenglieder 5:9-10:6:7.

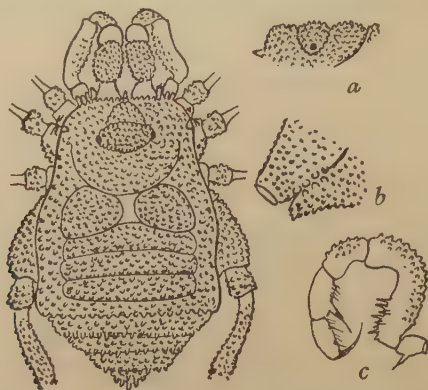


FIG. 1.—*Simienatus scotti*, gen. et sp. nov. ♂. Dorsalansicht des Körpers; (a) Stirnhügel und Tuber oculorum in linker Seitenansicht; (b) rechte 4. Coxa und Stigmensternit mit verdecktem Stigma in Ventralansicht; (c) linker Palpus in Seitenansicht.

Simienatus steht der Gattung *Djemia* (ebenfalls aus Abessinien) sehr nahe, ist von ihr doch leicht zu unterscheiden durch den Besitz einer sehr deutlichen Medianfurche der 1. Scutum-Area. Bei *Djemia* ist keine Spur, einer solchen Längsfurche zu bemerken.

ETHIOPIA (Abessinien). 'Simien: Mindigabsa, over 10,000 feet, 16. xi. 1952, from soil at roots of plants overhanging a stream, 1 ♂ (Type, in Brit. Mus.); Arghine, c. 11,500 ft., from peat-soil at roots of grass in ravine near torrent, 24. xi. 1952, 2 ♀, 2 juv. (Paratypes, in Brit. Mus.); same data as preceding, 1 ♂, 1 ♀ (Paratypes, Coll. Roewer)'.

Die bisher aus Abessinien bekannt gewordenen Opiliones verteilen sich auf folgende Arten und Gattungen:

Subord. OPILIONES LANIATORES.

Fam. Phalangodidae.

Subfam. BIANTINAE.

Hinzuanus africanus Pavesi, 1883. Schoa: Let-Marefia, 1 (♀ ?); *Ann. Mus. Civ. Genova*, 20, p. 88.

Fam. Assamiidae.

Subfam. ASSAMIINAE.

Gomezyta africana Roewer, 1935. Am Tana-See, 1 ♀; *Veroff. Deutsch. Kol. u. Übersee-Mus. Bremen*, 1 (1), p. 42.

Subfam. HARSADIINAE.

Harsadia spinosa Roewer, 1935. 'Lakes of Addas, shores of Hora Harsadi, 2-3. xii. 1926, 4 ♂, 2 ♀ (*J. Omer-Cooper*)'; *ibid.*, p. 43.

Argobba nigrescens Roewer, 1935. Argobba, ♂; *ibid.*, p. 44.

Subfam. ERECINAE.

Djemia cooperi Roewer, 1935. Djem-Djem Forest, ix-x. 1926, 3 ♂, 2 ♀ (*J. Omer-Cooper*); *ibid.*, p. 65.

Irnia scabra Roewer, 1935. Irna, ♂; *ibid.*, p. 69.

Simienatus scotti, spec. nov. ♂, ♀, juv. (vergl. oben).

Subfam. *POLYCORYPHINAE*.

Gulufia frontalis Roewer, 1935. Gulufa, ♂; *ibid.*, p. 91.

Subfam. *SIDAMINAE*.

Sidama moesta Pavesi, 1895. Arussi Galla, Ganale Gudda, ♂ oder ♀?; *Ann. Mus. Civ. Genova*, **35**, p. 531.

Sidama abessinica Roewer, 1912. Genaue Localität? ♂; *Arch. Naturg.* **78** (A, 3), p. 63.

Othmar gracillimus Roewer, 1935. Bei Harar, ♂; *Veröff. Deutsch. Kol. u. Übersee-Mus. Bremen* **1** (1), p. 99.

Anhara grata Pavesi, 1897. Gallaländer: Giari Bule, ♂ oder ♀? *Ann. Mus. Civ. Genova*, **38**, p. 185.

Orsimonia filipes Roewer, 1935. Östl. Tana-See, ♂; *Veröff. Deutsch. Kol. u. Übersee-Mus. Bremen*, **1** (1), p. 101.

Phezilbus spiniger Roewer, 1935. Bei Addis Abeba, ♂; *ibid.*, p. 103.

Subfam. *ACACINAE*.

Acaca albatra Roewer, 1935. Harar, ♂; *ibid.*, p. 140.

Subord. OPILIONES PALPATOIRES.

Fam. *Phalangiidae*.Subfam. *PHALANGIINAE*.

Cristina armata Roewer, 1911. Viele (♂, ♀, juv.); von Abessinien bis Ost-Afrika und Congo verbreitet; *Arch. Naturg.*, **77** (1, 2), p. 98. In der Coll. Scott befinden sich: Simien, Lori, 11,500 ft., 25. xi. 1952, 1 juv.; above Lori, c. 12,000 ft., from peat-soil at bases of stems of *Lobelia rhynchopetalum*, 28. xi. 1952, 1 ♀, 1 juv.; Walamo Province, Soddu, c. 6,800 ft., 21. x.-16. xi. 1948, 1 ♂.

Cristina zavattarii Caporiacco, 1939. Gallaländer: Lago Margherita u. Lago Zuai, ♂, ♀; *Missioni Biol. Pae-e Borana* (Reale Accademia Italia), **3**, p. 384.

Cristina subinermis Caporiacco, 1940. Gallaländer: Lago Margherita, ♀; *Atti Accad. Ital. (Mem.)*, **11** (18), p. 872.

Eudasylobus denticulatus (Kulcz.) 1901. Massaua-Ghinda, ♂, ♀; *Rozpr. Ac. Krakow*, **41** (B), p. 56.

Novabunus spinosus Goodnight, 1944. Genaue Localität?? ♂, ♀; *Amer. Mus. Novit.* **1255**, p. 4.

Rhampsinitus pachylomerus (Simon), 1879 (sub *Egaenus*). Genaue Localität??, ♂, ♀; *Ann. Soc. Ent. Belg.*, **22**, C.R., p. 70.

Rhampsinitus somalicus Caporiacco, 1927. Süd-Somaliland: Darod, ♂; *Monit. Zool. Ital.*, **38** (a), pl. 234.

INSECTA DIPLURA, JAPYGIDAE, FROM ETHIOPIA. By JEAN PAGÉS,
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(Communicated by HUGH SCOTT, Sc.D., F.R.S., F.L.S.)

(With 27 text-figures.)

[Read 21 October 1954.]

Silvestri (1948) a déjà décrit 3 formes d'Éthiopie ; il les a placées dans 2 genres qui ne sont jusqu'à présent connus que de ce pays et dont les ♂ sont caractérisés par leurs appendices génitaux terminés par une cornicule : *Proncojapyx scotti* d'Addis Ababa, *Proncojapyx scotti* var. *nermoralis* de la Djem-Djem Forest, *Xenjapyyx bouvieri* de Hiéka (pour la situation géographique de cet endroit, voir la note ci-dessous).

M. le Dr. Hugh Scott que je tiens à remercier ici, a bien voulu me confier l'étude de 4 exemplaires récoltés par lui en 1948 et 1952 dans cet empire. Ils représentent 3 espèces inédites dont une a nécessité la création d'un genre nouveau : (?) *Afrojapyyx mixtus*, *Xenjapyyx tolaianus*, *Scottojapyyx simienensis*, gen. n., sp. n.

La diagnose du genre nouveau et la description des espèces nouvelles font l'objet de cette note.*

(?) *Afrojapyyx mixtus*, sp. nov. (Figs. 1-6).

♂. TÊTE. *Vertex* : 10 + 10 soies longues sur 3 + 3 rangées longitudinales de respectivement 4, 4 et 2 soies pour chaque moitié en partant de la ligne médiane ; 7 + 7 soies assez courtes ou courtes et de peu nombreuses très courtes. *Antennes* de 34 articles assez pileux. 13 trichobothries typiques, *a* † légèrement proximale. 8 sensilles placoides en position typique sur l'article apical. *Maxilles* : les 5 lames du lobe interne sont pectinées ; pas d'épine à la base de la 3e lame. *Labium* : lobe externe pileux ; la soie antérieure de l'angle interne est sinueuse, simple, très légèrement plus épaisse que les autres soies de ce sclérite. Lobe interne pourvu d'une minuscule soie. *Mentum* typique, c'est-à-dire présentant un groupe antérieur

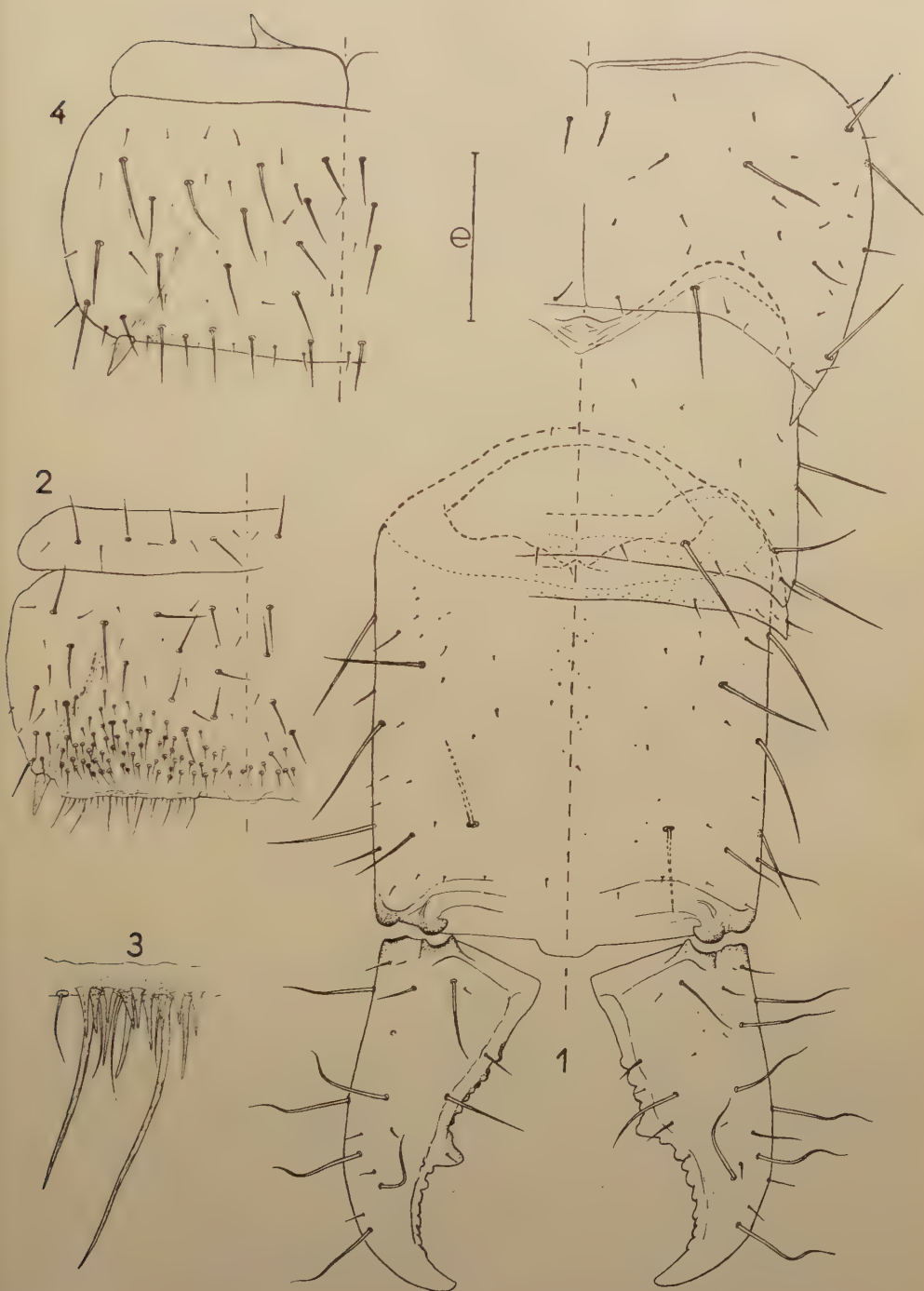
* [The author describes the Japygidae collected during my two recent journeys in Ethiopia. A new species of *Xenjapyyx*, and a new species provisionally referred to *Afrojapyyx*, were discovered in the Gughé Highlands (Southern Ethiopia), at about 10,600 feet, in 1948 ; while a form constituting a monotypic new genus and species was found in high Simien (Northern Ethiopia), above 10,000 feet, in 1952.

Simien and the Gughé Highlands are roughly 500 miles apart. But the three forms previously described by Silvestri (1948) were found in intermediate places, at rather lower altitudes. Two of these, a species and a named variety of *Proncojapyyx*, were collected by myself and Professor Omer-Cooper during our joint expedition in 1926, respectively at Addis Ababa and in Jem-Jem Forest, in both cases at about 8,000 feet. The third, *Xenjapyyx bouvieri* (originally placed in *Japyyx*), was discovered by Baron Maurice de Rothschild on 31 March 1904 at Hiéka, a small place over 35 miles W.N.W. of Harar, at about 6,650 feet (the situation of Hiéka and a number of other places is given in *Voyage de M. le Baron Maurice de Rothschild en Éthiopie et en Afrique orientale anglaise 1904-5* ; the *Résultats scientifiques, Animaux Articulés* (published 1922) contain an alphabetic list of localities with dates in the *Première Partie* (p. xiv), and a map at the end of the *Deuxième Partie*).

None of the five species now known from Ethiopia has been recorded from outside that country.

The Diplura, recently raised to ordinal rank, were formerly included in Thysanura as the sub-order Entognatha, comprising the families Japygidae and Campodeidae.—H.S.]

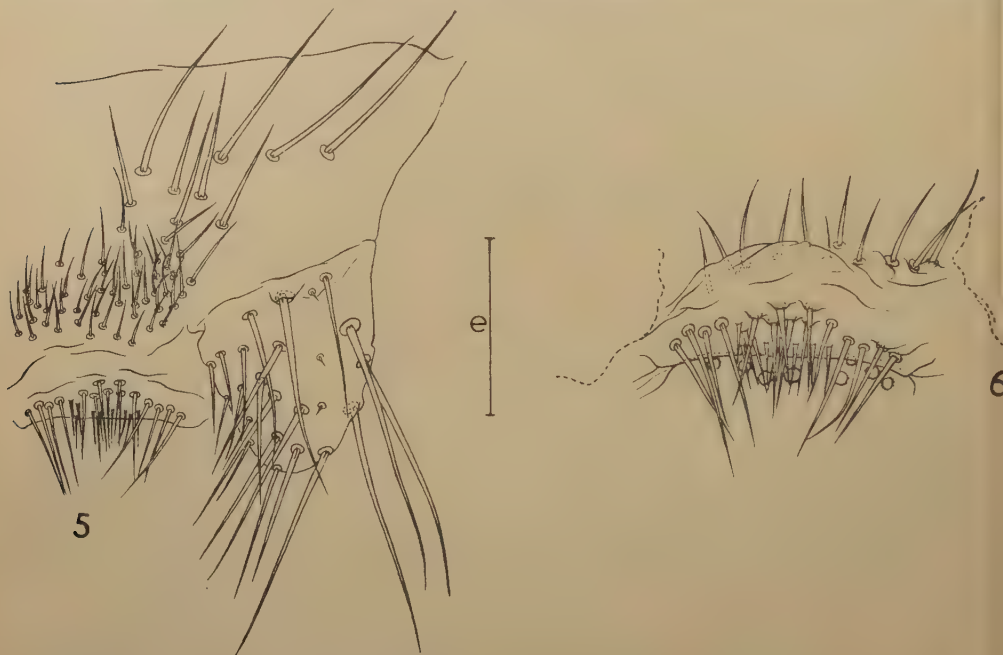
† ABBRÉVIATIONS : *a* = trichobothrie tergale submédiane du 4e article antennaire ; P I, P II, P III = 1e, 2e, 3e paire de pattes ; *M*, *m* = macrochète et submacrochète, la lettre ou le chiffre qui suivent ces sigles en indique la position sur les tergites (cf. Pagés, 1954) ; *A*, *B*, *C* = rangée antérieure, intermédiaire et postérieure de *M* sur les urosternites (cf. Pagés, 1954) ; *st* et *s* = style et la soie antérieure typique, le chiffre en indice désigne l'urosternite ; *r* = rapport obtenu en divisant les longueurs : " angle basal interne d'un cerque-dent " et " dent-apex d'un cerque ".



(?) *Afrojapyx mixtus*, sp. nov. 1. Urotergites 7 à 10 et les cerques, $e = 250 \mu$. 2. Urosternite 1, $e = 250 \mu$. 3. Détail d'un organe subcoxal latéral, $e = 44 \mu$. 4. Urosternite 3, $e = 250 \mu$.

et un groupe postérieur de soies, chacun d'eux composé d'une soie nettement plus longue et insérée plus latéralement que les autres qui sont massées principalement le long de la suture médiane. Palpes labiaux près de 2 fois aussi longs que larges à la base, portant, outre le sensille apical, 2 soies subapicales près de 1 fois $7/10$ aussi longues que le palpe qui les porte, 6 soies sur la face antérieure et 1 minuscule soie insérée sur la $1/2$ basale de la face postérieure.

THORAX. *Pronotum* : $5 + 5 M$, M_3 les plus longs ; $5 + 5$ soies assez courtes. *Mesonotum* : préscutum, $1 + 1 M$ assez longs et $1 + 1$ soies assez courtes ; scutum, $5 + 5 M$ longs, $1 + 1$ soies insérées au-dessus de l'embase des M_3 aussi longues que les M_1 mais sans l'embase caractéristique des M ; environ $10 + 10$ soies assez courtes. *Metanotum* : préscutum, $1 + 1 M$, $1-2 + 1-2$ soies assez courtes ou courtes ; scutum, $5 + 5 M$ longs et $5 + 5$ soies assez courtes ou courtes. *Pattes*



(?) *Afrojapyx mixtus*, sp. nov. 5. Partie antérieure gauche et l'appendice génital correspondant $e = 60 \mu$. 6. Orifice génital, l'aire postérieure de soies courtes n'a été indiquée que par les embases des 8 soies courtes les plus voisines de l'orifice génital ; en pointillé l'emplacement des appendices génitaux ; $e = 44 \mu$.

assez pileuses ; soies sternales spiniformes des tarses au nombre de : (1) $4 + 4$ aux PI ; (2) $8 + 8$ aux PII et PIII ; les plus antérieures de ces soies sont moins différenciées que les autres ; prétarses bien développés, typiques.

ABDOMEN. *Tergite 1* : préscutum, $1 + 1 M$ longs ; scutum, $1 + 1 M$ (M_5) longs et quelques soies courtes. *Tergite 2* : $4 + 4 M$ ($ma = M$, M_1 , M_4 , M_5) longs ; msa , m_2 et m_3 subégaux, courts, plus longs que les mi ; m_1 subnuls. *Tergites 3 à 7* : $6 + 6 M$ ($ma = M$) ; msa et m_3 subégaux, courts, plus longs que les mi ou m_2 ; m_1 les plus petits de tous ; la taille des mi croît du 1^{er} au dernier de ces tergites alors que celle des autres m tend plutôt à décroître ; en outre de rares soies très courtes. *Tergite 8* : 1 fois $11/25$ aussi large que long ; $4 + 4 M$ dont $1 + 1$ latéraux intermédiaires et $3 + 3$ postérieurs ; $1 + 1$ soies assez courtes latérales intermédiaires, $1 + 1$ assez courtes latérales postérieures et $3-4 + 3-4$ autres très courtes. *Tergite 9* près de 3 fois aussi large que long, sans M . *Tergite 10* environ 1 fois $1/3$ aussi long que

large au niveau de ses angles latéraux antérieurs, sa largeur au niveau des angles latéraux postérieurs étant légèrement plus faible : $5 + 5 M$ longs dont $2 + 2$ discaux et $3 + 3$ latéraux, $1 + 2$ soies sublatérales subpostérieures assez longues, $3 + 2$ soies latérales assez courtes et quelques autres très courtes. *Acropyge* peu élevé, trapézoïdal, à angles arrondis. *Angles latéraux postérieurs des tergites* : nuls du 1^{er} au 6^e tergite ; ceux du 7^e en pointe aiguë, triangulaire, plus longue que large à sa base, bien séparée du reste du tergite ; ceux du 8^e et du 9^e tergites subdroits.

Sternite 1 : préscutum, $4 + 4 M$ longs, $5 + 5$ soies courtes ; scutum, $16 + 16 M$ longs dont les $13 + 13$ typiques, $2 + 2$ entre A_1 et B_4 et $1 + 1$ entre B_1 et C_1 ; on remarquera que la rangée des B est très fortement arquée vers l'arrière et que les B_3 sont beaucoup plus près des C_2 qu'habituellement ; environ $18 + 18$ soies assez courtes ou courtes ; soies à embase circulaire caractéristique peu différenciées, formant une plage triangulaire limitée par les C_1 , B_4 et C_3 .

Organes subcoxaux latéraux saillants, occupant environ le 1/3 de la largeur inter-styloire : 82 soies glandulaires sur l'organe droit, 71 sur le gauche, de tailles très inégales : par organe il y en a : (1) 6-7 valant les 117/100 de la longueur de st_1 ; (2) 5 en égalant les 78 100 ; (3) 13-16 les 33 100 ; (4) 46-55 dont la taille est comprise entre les 12 100 et 20 100 de la même mesure. L'appareil glandulaire n'a pu être observé convenablement : il semble que tous les canaux soient sensiblement de la même longueur et terminés par un petit réservoir ovoïde ; 22-23 soies sensorielles valant en moyenne les 46/100 de la longueur de st_1 ; elles paraissent inégales, les limites extrêmes de mes mesures étant 40 100 et 61/100, mais je n'ai pu m'assurer s'il en est bien ainsi ou si ce n'est qu'un artefact.

Organe glandulaire médian bien développé, saillant ; opercule avec $1+1$ soies extrêmement courtes sur sa ligne d'articulation et 6 autres encore plus courtes sur son bord libre. Je n'ai vu aucun orifice glandulaire.

Sternites 2 à 7 : $17 + 17 M$ différenciés longs, B_4 et les C de rang pair indifférenciés, assez longs, ainsi qu'une vingtaine de soies réparties sans ordre apparent sur tout le sclérite ; on remarquera que s'il est relativement facile d'homologuer les A et les B , il n'en est plus de même pour les C : chaque moitié de cette rangée est, en effet, composée de 6 M et de 6 soies assez longues, ce qui donne un total de 12 phanères au lieu de 10 ; on peut assez aisément repérer les C_3 à C_{10} d'après leurs positions par rapport au style et à la vésicule, ainsi que les C_1 , qui sont les plus médians ; le M restant est alors peut-être le C_2 , à moins que ce dernier ne soit indifférencié et que cette paire de M soit supplémentaire.

Pas de *fossettes glandulaires*.

Styles peu aigus ; cône secondaire très petit, tuberculiforme, pore énigmatique bien visible ; $st_1/st_7=0,82$; $s_1/s_7=0,80$; $s_1/st_1=0,22$; $s_1/st_7=0,18$.

Vésicules exsertiles petites, présentes du 1^{er} au 7^e sternite.

Papille génitale ♂ ; les soies courtes de l'aire antérieure sont divisées en 2 groupes : (1) le premier s'étend entre les appendices et ses soies sont plus nombreuses à ses extrémités qu'en son milieu sans cependant former 2 plages comme chez *Congjapyx* Pagés ; (2) le second est situé immédiatement en avant de l'orifice génital et est constitué par 15 soies subuniséries, plus longues que celles du groupe précédent, suivies d'une rangée de soies courtes, sans embase. Aire postérieure typique. Appendices génitaux assez pileux, entièrement membraneux, courts, leur longueur égalant leur écartement ; face antérieure avec 22 soies disposées comme à l'accoutumée, c'est à dire que plus elles sont implantées près de l'angle basal interne, plus elles sont courtes et que plus elles sont situées près de l'extrémité distale, plus elles sont longues ; ici les plus longues égalent 1 fois 1/4 la longueur d'un appendice et les plus courtes le 1/3 seulement ; on remarquera 3 soies extrêmement courtes, insérées à une faible distance du bord externe. Face postérieure glabre.

Longueurs relatives des segments 7 à 10 : 46-57-23-100.

CERQUES : plus courts d'environ 1/6 que la partie normalement découverte du tergite 10 (21/25), près de 2 fois aussi longs que larges à la base (19/10) ; assez arqués

et peu aigus. *Cerque droit* armé d'une forte dent obtuse, très légèrement post-médiane, $r=1,09$; marge prédentale rectiligne avec 4 tubercules arrondis, contigus ; marge postdentale concave avec 9 forts denticules arrondis. *Cerque gauche* armé d'une forte dent triangulaire obtuse, postmédiane, $r=1,59$; marge prédentale subrectiligne avec 4-7 petits tubercules arrondis, régulièrement espacés ; marge postdentale concave avec $\frac{1}{3}$ denticules arrondis, le supérieur est très petit, situé au-dessus du 1^{er} denticule inférieur.

Longueur du spécimen, 7.5 mm.

ÉTHIOPIE : Gamo Province, Gughé Highlands, sur le Mt. Tola, à une altitude d'environ 10,600 pieds, Décembre 1948, 1 ♂, dans les racines (Scott).

AFFINITÉS : je rapproche provisoirement cette forme des *Afrojapyx* Silv., dont elle possède une chétotaxie tergale comparable, les organes glandulaires postérieurs du 1^{er} urosternite, les appendices génitaux entièrement membraneux et des cerques d'une forme semblable. Le nombre d'articles antennaires de *mixtus* est celui indiqué pour la var. *modestior* Silv. du génotype *Afrojapyx stricklandi* Silv., provenant du Gold Coast.

Elle s'écarte des *Afrojapyx* typiques par : (1) la présence d'une seule rangée de tubercules à droite au lieu de 2 ; (2) la présence d'un denticule supérieur à gauche, ce qui la rapproche des genres *Oncojapyx* Silv. du Congo belge et de l'Angola, et *Proncojapyx* Silv. d'Éthiopie ; sa papille génitale ♂ a une chétotaxie qui ressemble beaucoup à celle de *Xenjapyx* Silv. d'Éthiopie, et elle est construite sur le même modèle que celle de *Congjapyx* Pagés du Congo belge, mais chez ce dernier genre, le premier groupe de soies courtes de l'aire antérieure est nettement formé de 2 plages séparées et il n'y a pas de soies sans embase en avant de l'orifice génital.

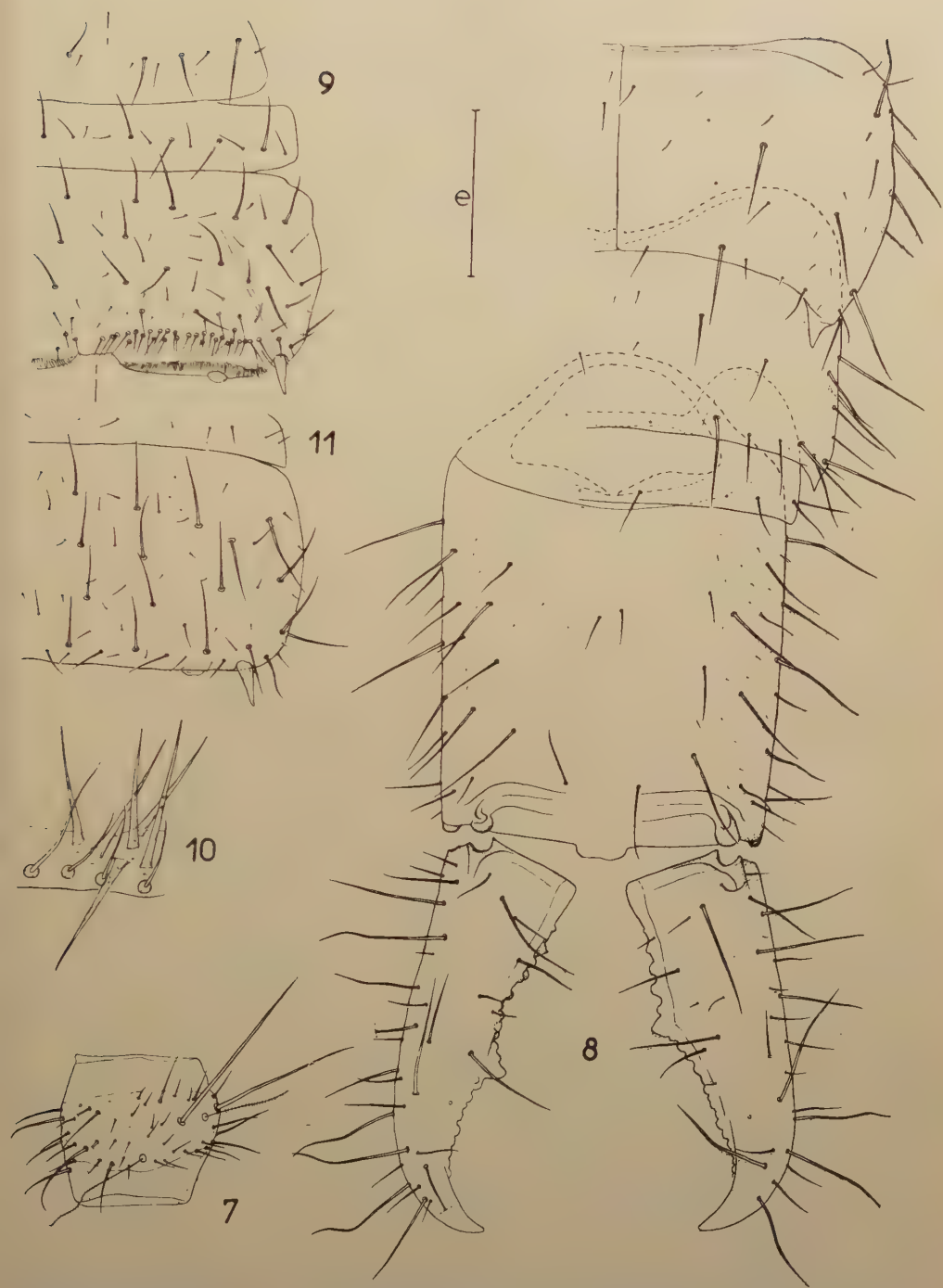
Ces divers caractères permettent de reconnaître sans ambiguïté cette espèce, pour laquelle il sera peut-être nécessaire de créer une coupe générique quand les Japygidés africains seront mieux connus.

Xenjapyx tolaianus, sp. nov. (Figs. 7-13).

♂. TÊTE. *Vertex* : 20 + 20 soies longues disposées sur 4 + 4 rangées longitudinales, comptant chacune 5 soies ; 3-4 + 3-4 soies courtes et de rares autres très courtes. *Antennes* de 45 articles recouverts de nombreuses soies courtes et de quelques soies longues. Aires pileuses indistinctes. 13 trichobothries typiques, *a* est très nettement proximale. 8 sensilles placoides en position typique sur l'article apical. *Maxilles* : les 5 lames du lobe interne sont pectinées ; 1 épine courte à la base de la 3^e lame. *Labium* : lobe externe pileux ; la soie de son angle interne antérieur n'est pas différente des autres. Lobe interne avec 1 soie très courte. *Mentum* typique. *Palpes labiaux* près de 2 fois $1/5$ aussi longs que larges à la base, portant 2 soies subapicales, 1 fois $1/10$ à 1 fois $2/10$ aussi longues que le palpe qui les porte, et 8 autres soies longues ou courtes sur sa face antérieure, 1 soie très courte sur sa face postérieure.

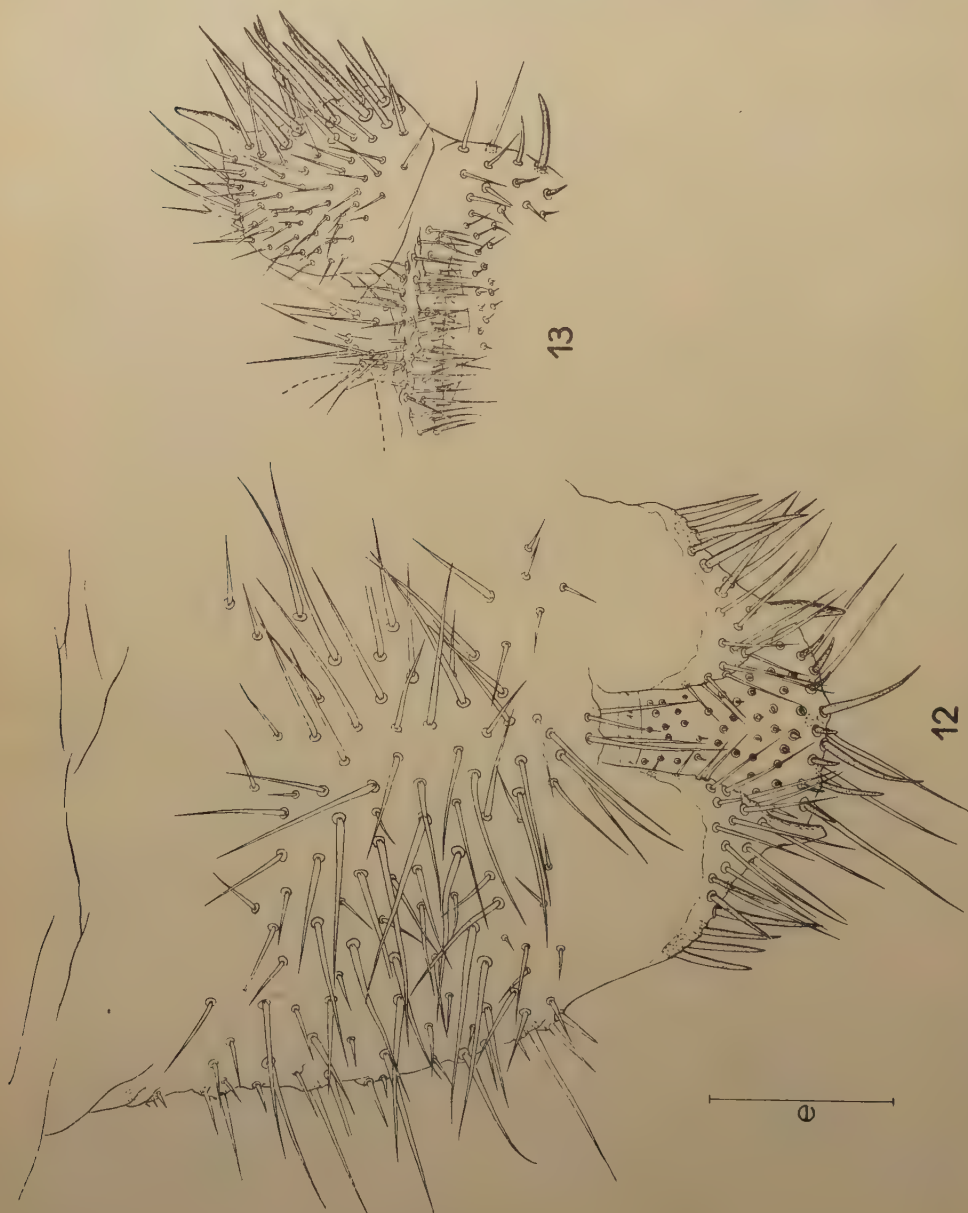
THORAX. *Pronotum* : les 5 + 5 *M* typiques longs, 4-5 + 4-5 soies assez longues ou courtes. *Mesonotum* : préscutum, 1 *M* assez long sur sa $1/2$ gauche et de nombreuses soies très courtes ; scutum, 6 + 6 *M*, les 5 + 5 typiques et 1 + 1 supplémentaires au-dessus de l'insertion des *M*₃, 10 + 10 soies assez longues ou courtes. *Metanotum* : préscutum, 1 + 1 *M* assez longs, 1 + 1 soies courtes ; scutum, 5 + 5 *M* longs, 7 + 7 soies assez longues ou courtes. *Pattes* pileuses surtout sur les fémurs ; 4 + 4 soies sternales spiniformes aux tarses des P I et P II, 5 + 5 de ces soies aux P III. Pré-tarses bien développés.

ABDOMEN. *Tergite 1* : préscutum, 1 + 1 *M* longs ; scutum, 1 + 1 *M* (*M*₅) longs et 4-5 + 4-5 soies courtes. *Tergite 2* : 4 + 4 *M* (*ma*=*M*, *M*₁, *M*₄, *M*₅) longs ou assez longs ; *m*₃, *m*₂ et *mi* subégaux aux *ma* ; *m*₁ courts ainsi que le *msa* droit, le seul présent ; 4 + 4 soies courtes et quelques autres très courtes, réparties sans ordre apparent sur le sclérite. *Tergites 3 et 4* : 6 + 6 *M* (*ma*=*M*) ; *msa*, *m*₂, *m*₃



Xenjapyx tolaianus, sp. nov. 7. Face tergale du 4^e article de l'antenne droite, $e = 250 \mu$.
 8. Urotergites 7 à 10 et les cerques, $e = 444 \mu$. 9. Urosternite 1, $e = 444 \mu$. 10. Détail
 d'un organe subcoxal latéral, $e = 44 \mu$. 11. Urosternite 3, $e = 444 \mu$.

et m_i subégaux assez courts, plus longs que m_1 ou m_4 ; 4 + 4 soies courtes. *Tergites* 5 à 7 : 5 + 5 M , les ma n'étant pas différenciés en M ; le reste identique aux 2 tergites précédents. *Tergite* 8 : 1 fois 4/5 aussi large que long ; 4 + 4 M longs dont 1 + 1 latéraux antérieurs, 1 + 1 latéraux postérieurs, 1 + 1 sublatéraux postérieurs,



Xeniparus tolaianus, sp. nov. 12. Papille génitale ♂, les appendices génitaux sont rabattus vers l'arrière, $e = 142 \mu$. 13. Papille génitale ♂, les appendices génitaux sont rabattus vers l'avant découvrant ainsi l'orifice génital, $e = 142 \mu$.

1 + 1 submédians postérieurs ; 9 + 9 soies longues dont 1 + 1 submédianes antérieures et 4-5 + 4-5 autres courtes. *Tergite* 9 près de 2 fois 7/10 aussi large que long, sans M mais avec 5 + 5 soies tergaes assez longues. *Tergite* 10 près de 1 fois 1/2

aussi long que large au niveau des M latéraux antérieurs : $3 + 3 M^*$ longs, $8 + 9$ soies longues et $5 + 6$ soies courtes ; en outre de nombreuses soies très courtes réparties sans ordre apparent sur tout le sclérite. *Acropyge* bien développé, subrectangulaire, à angles postérieurs arrondis. *Angles latéraux postérieurs des tergites* : nuls du 1^{er} au 6^e tergite ; ceux du 7^e et du 8^e en pointe aiguë, triangulaire, à peu près aussi longue que large à sa base ; ceux du 9^e droits.

Sternite 1 : préscutum, $4 + 4 M$ longs, $5 + 1 + 5$ soies assez longues ou courtes ; scutum, les $13 + 13 M$ typiques longs, sauf les B_5 qui sont moins différenciés que les autres ; de très nombreuses soies courtes ou assez courtes réparties sans ordre apparent entre les M : une soixantaine de soies, à embase circulaire caractéristique, assez longues, formant 2 rangées irrégulières en avant des organes glandulaires postérieurs.

Organes subcoxaux latéraux occupant chacun les 2/5 de la largeur interstylière ; environ 140 soies glandulaires dont la longueur est comprise entre les 29/100 et les 39/100 de celle de st_1 , la moyenne en étant les 32/100 ; l'appareil glandulaire n'a pu être observé. 36 soies sensorielles dont les tailles extrêmes valent les 20/100 et les 30/100 de la longueur du st_1 , la moyenne en étant les 27/100.

Organe glandulaire médian très rudimentaire, et il est impossible sur cet exemplaire de reconnaître avec certitude un opercule et une membrane ; sur la convexité qui correspondrait à l'opercule se trouvent $1 + 7 + 1$ soies très courtes, les soies médianes formant une double rangée longitudinale. Je n'ai vu aucun orifice glandulaire.

Sternites 2 à 7 : $16 + 16 M$ différenciés longs ; B_4 et tous les C de rang pair indifférenciés, assez longs ; C_8 et C_{10} plus longs que les autres C pairs ; une vingtaine de soies courtes ou très courtes réparties sans ordre apparent sur tout le sclérite.

Styles assez allongés ; cône secondaire arrondi, petit ; pore énigmatique bien visible ; $st_1/st_7=0,74$; $s_1/s_7=0,76$; $s_1/st_1=0,18$; $s_1/st_7=0,13$.

Vésicules exsertiles petites, présentes du 1^{er} au 7^e urosternite.

Papille génitale ♂ très pileuse, allongée. La base montre de très nombreuses soies de toutes tailles, formant une couronne continue antérieure. L'aire antérieure de soies courtes n'est pas visible lorsque les appendices sont rabattus vers l'arrière ; elle est constituée par 3-4 rangées de soies à embase et d'une vingtaine de soies très courtes sans embase, formant une rangée irrégulière en avant de l'orifice génital. Le bord postérieur de cet orifice porte $1 + 3 + 3 + 1$ soies très courtes sans embase. Les soies courtes de l'aire postérieure sont espacées, plus ou moins spiniformes, colorées, augmentant de taille vers l'arrière et sur les bords. Toutes les soies dont il vient d'être question ne sont pas parfaitement symétriques par rapport à leur axe, mais présentent sur leur face postérieure un élargissement près de leur embase. Appendices génitaux courts, trapus, subquadrangulaires, terminés par un fort crochet coloré ; la distance qui les sépare égale le 1/3 de leur largeur à la base ; face antérieure glabre ; la postérieure montrant des soies assez longues, colorées, spiniformes, sur le bord externe et des soies ordinaires assez courtes ou courtes sur tout le reste de la surface.

Pas de fossettes glandulaires.

Longueurs relatives des segments 7 à 10 : 40-50-28-100.

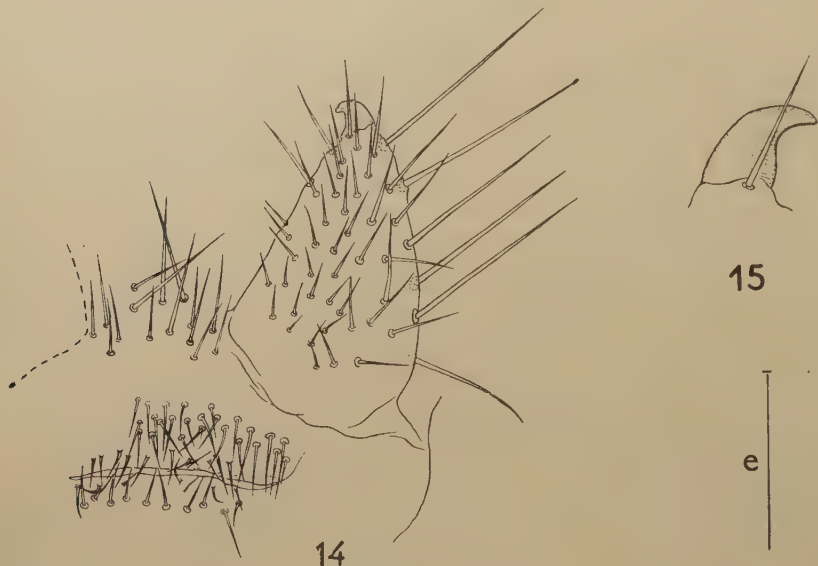
CERQUES : aussi longs que la partie normalement découverte du tergite 10, un peu plus de 2 fois 1/2 aussi longs que larges à la base, peu arqués, aigus.

Cerque droit armé d'une forte dent triangulaire prémédiane, $r=0,75$; marge prédentale très légèrement concave, avec 5 tubercules arrondis, le plus proximal

* Je considère comme M , outre les phanères dont l'embase correspond à celle que j'ai indiquée comme caractéristique de ces phanères, ceux dont la tige paraît pleine et lisse (*homogène*), alors qu'une soie montre toujours plus ou moins nettement le canal médullaire ou des carènes longitudinales (*hétérogène*) ; un M typique possède ces 2 caractères ; les *ma*, quand ils acquièrent l'embase caractéristique des M , deviennent homogènes ; je n'ai encore jamais trouvé de submacrochètes qui seraient homogènes avec une embase de soie ou des M à embase caractéristique qui seraient hétérogènes. Je considère donc pour l'instant que lorsqu'il n'est pas possible d'observer convenablement l'embase d'un phanère sur le tergite 10 ou sur les régions latérales du tergite 8, par exemple, qu'il s'agit d'un M si sa structure est homogène et d'une soie dans le cas contraire.

très petit, les autres assez gros ; marge postdentale légèrement concave avec 15-16 denticules arrondis de tailles irrégulières. *Cerque gauche* armé d'une forte dent triangulaire postmédiane, $r = 1,30$; marge prédentale légèrement concave avec 5,8 tubercules, tous arrondis sauf les 2 proximaux de la rangée inférieure ; les 2 supérieurs distaux sont contigus ; marge postdentale concave avec 1/9 denticules arrondis, de tailles irrégulières, plus petits vers l'apex du cerque que vers la dent.

Longueur du spécimen, 12 mm.



Xenjapyx bouvieri Silv. ♂ type de Hiéka. 14. Orifice génital et appendice gauche rabattu vers l'avant, e = 100 μ . 15. Crochet terminal de l'appendice génital droit, e = 44 μ .

ÉTHIOPIE : Gamo Province, Gughé Highlands, sur le Mt. Tola, à une altitude d'environ 10,600 pieds, Décembre 1948, 1 ♂, dans les racines (Scott).

AFFINITÉS : cette espèce est voisine de *Xenjapyx bouvieri* Silv. (Figs. 14, 15), connu par un seul exemplaire récolté en Éthiopie à Hiéka. On séparera ces 2 espèces par : (1) le nombre d'articles antennaires ; (2) la chétotaxie tergale des urotergites ; (3) l'absence de carènes sur le tergite 10 de *tolaianus* ; (4) la structure des organes subcoxaux latéraux dont, les soies glandulaires sont multisériées vers l'extérieur et unisériées vers l'intérieur chez *bouvieri*, subunisériées sur toute la largeur de l'organe chez *tolaianus* ; (5) la forme et la chétotaxie des appendices génitaux ; je donne un dessin de cet appendice fait d'après le type de *bouvieri* conservé au Muséum d'Histoire naturelle de Paris, et qui m'a été aimablement communiqué par M. le Professeur L. Chopard.

SCOTTOJAPYX, gen. nov.

Appartient à la sous-famille des *Japyginae* Womersley.

TÊTE et THORAX typiques.

ABDOMEN. Chétotaxie des tergites et sternites typique. Angles latéraux postérieurs du 7e tergite bien individualisés, transformées en un appendice séparé du reste du tergite. Organes subcoxaux latéraux typiques, munis d'une seule rangée de soies glandulaires de tailles très inégales et d'une rangée de soies sensorielles. Organe glandulaire médian typique ; l'opercule porte 2 soies sur sa ligne d'articulation et un certain nombre de soies microscopiques ("pseudoporis" de Silvestri) sur sa partie

distale. Membrane sans aucun orifice glandulaire décelable. *Papille génitale* ♂ : appendices génitaux entièrement membraneux, petits : aire antérieure de soies courtes très réduite, précédant une plage de soies sans embase localisées sur la face tergale d'une profonde invagination située en avant de l'orifice génital : aire postérieure de soies courtes très dense, limitée du côté de l'orifice génital par une rangée de soies sans embase.

CERQUES : allongés, symétriques, sans dents. Marges internes rectilignes, celle de droite avec 2 rangées de denticules, les supérieurs très petits, celle de gauche avec une seule rangée de denticules.

AFFINITÉS : ce genre est très voisin de *Japygianus* Silv. d'Australie, dont il se distingue par l'ensemble des caractères indiqués ci-dessus. La chétotaxie tergale et la forme des cerques permettent de séparer sans difficulté *Scottojapyx* de *Japygellus* Silv., du Nigéria.

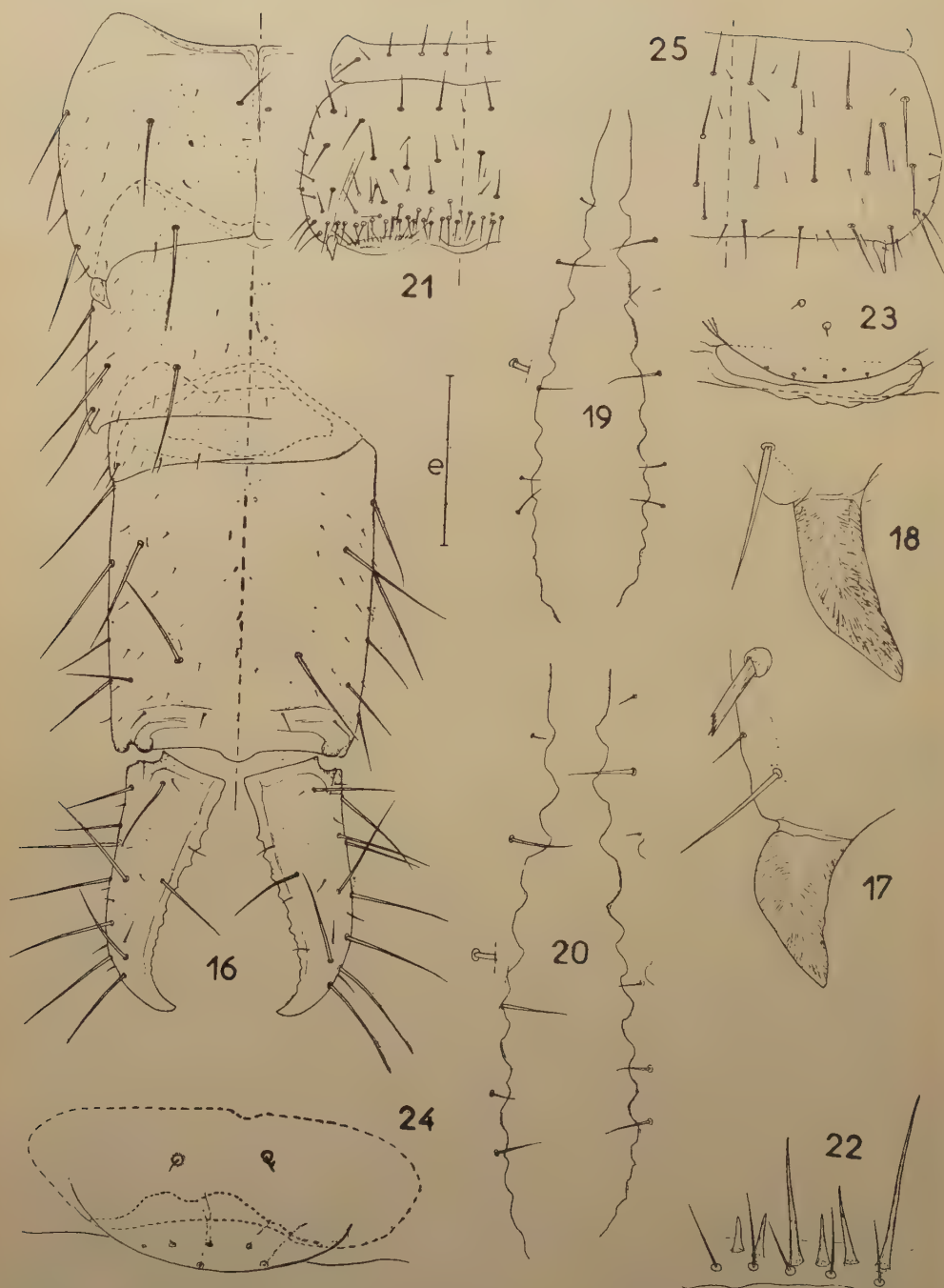
Espèce typique : *Scottojapyx simienensis*, sp. nov.

Scottojapyx simienensis, sp. nov. (Figs. 16-27).

♂♀. *TÊTE*. *Vertex* : 11 + 11 soies disposées sur 3 + 3 rangées longitudinales de respectivement 4, 4, 3 soies pour chaque moitié, en partant de la ligne médiane ; environ 10 + 10 soies courtes et quelques autres très courtes réparties sans ordre apparent sur le sclérite. *Antennes* de 28 articles assez pileux ; les 13 trichobothries typiques, *a* est à égale distance des 2 extrémités du 4^e article ; six sensilles placoides en position typique sur l'article apical. *Maxilles* : la 1^{re} lame du lobe interne est entière, les 4 autres pectinées ; une 1 épine à la base de la 3^e lame. *Labium* : lobe externe pileux ; la soie située dans l'angle interne est fortement arquée, nettement barbelée sur ses 3 4 distaux. Lobe interne avec une soie minuscule. *Palpes labiaux* environ 2 fois 1 5 aussi longs que larges à la base ; portant 8 soies sur la face antérieure, dont les 2 subapicales sont environ 1 fois 1/5 aussi longues que le palpe qui les porte ; face postérieure sans phanère visible ; près de la base, sur le bord externe, j'ai observé une structure ressemblant à une embase de soie, mais je n'ai pu y distinguer aucun phanère.

THORAX. *Pronotum* : 5 + 5 *M* longs ; chez le ♂ il en existe un 6^e inséré entre les *M*₂ et *M*₃ gauches ; 5-7 + 5-7 soies assez longues. *Mesonotum* : préscutum, 1 + 1 *M* assez longs ; chez le ♂ on observe en outre 1 + 1 soies courtes ; scutum, 6 + 6 *M*, les supplémentaires insérés au-dessus des embases des *M*₃ et plus courts que tous les autres *M* ; 5-6 + 5-6 soies assez courtes ou très courtes. *Metanotum* : préscutum avec 1 + 1 *M* ; scutum avec les 5 + 5 *M* typiques. *Pattes* assez pileuses ; 8 soies spiniformes sternales aux tarses de toutes les pattes, la paire la plus antérieure pouvant faire en partie ou entièrement défaut. *Prétarses* typiques, bien développés ; l'unguiculus aigu, long, est bien dégagé des griffes qui sont allongées, aiguës.

ABDOMEN. *Tergite 1* : préscutum, 1 + 1 *M* ; scutum, 2 + 2 *M* (*ma* = *M*, *M*₅) ; les *msa* sont très petits mais bien reconnaissables ; en outre quelques soies assez courtes. *Tergite 2* : 4 + 4 *M* (*ma* = *M*, *M*₁, *M*₄, *M*₅) longs ; *msa* très petits ; *m*₁ *m*₂ et *m*₃ assez courts, les *m*₁ les plus courts. *Tergites 3 à 7* : 6 + 6 *M* (*ma* = *M*) longs ou assez longs ; *msa* toujours très petits, paraissent plus longs chez la ♀ que chez le ♂ ; *m*₁ courts, *m*₂ et *m*₃ assez courts, les *m*₂ les plus longs de tous ; en outre de très nombreuses soies très courtes réparties sans ordre apparent sur tous les tergites. *Tergite 8* : un peu moins de 1 fois 4/5 aussi large que long, 4 + 4 *M* longs dont 1 + 1 submédians postérieurs, les autres latéraux. *Tergite 9* : un peu plus de 2 fois 4/5 aussi large que long ; pas de *M* mais une rangée postérieure de soies un peu plus développées que les autres. *Tergite 10* : 1 fois 1/2 aussi long que large au niveau des *M* latéraux antérieurs chez le ♂, 1 fois 2/5 seulement chez la ♀ ; pas de carènes ; 5 + 5 *M* longs dont 2 + 2 discaux et 3 + 3 latéraux ; 2 + 2 soies latérales assez longues, localisées sur le 1/3 distal du segment ; de nombreuses soies courtes et très courtes réparties sans ordre apparent sur tout le sclérite. *Acropyge* en demi-ellipse,

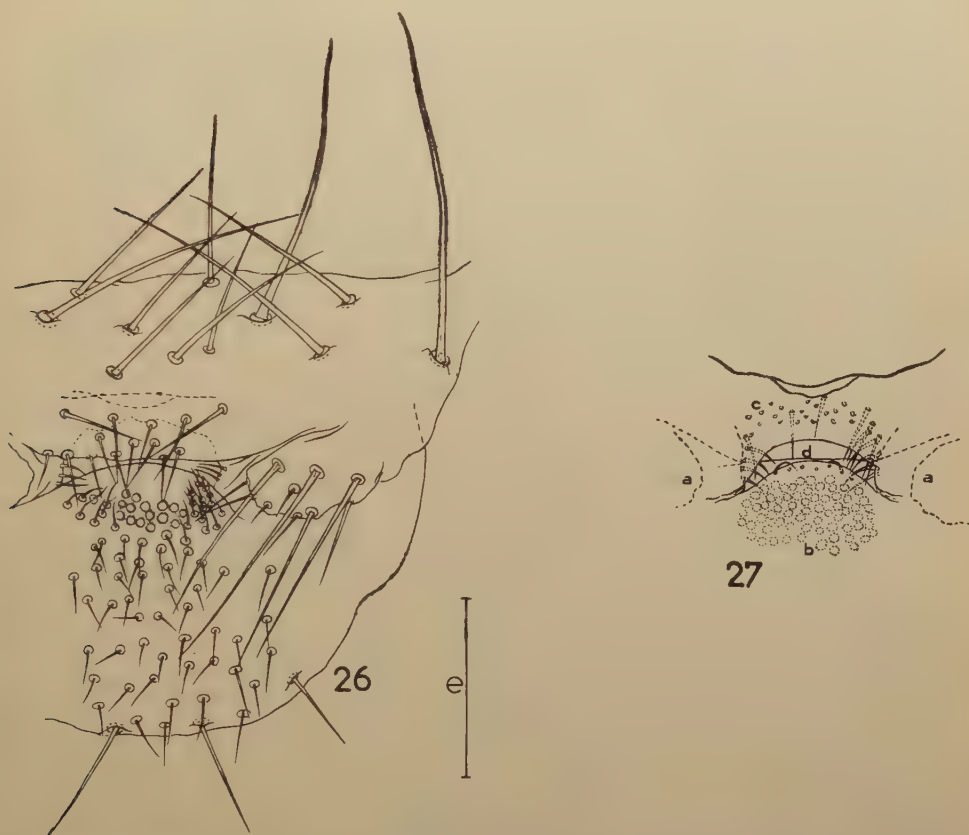


Scottojapyx simienensis, gen. et sp. nov. 16. Urotergites 7 à 10 et les cerques, $e = 250 \mu$. 17. Angle latéral postérieur gauche du σ , $e = 56 \mu$. 18. Angle latéral postérieur gauche de la φ , $e = 56 \mu$. 19. Détail des marges internes des cerques du σ , $e = 100 \mu$. 20. Détail des marges internes des cerques de la φ , $e = 100 \mu$. 21. Urosternite 1, $e = 250 \mu$. 22. Détail d'un organe subcoxal latéral, du σ , $e = 44 \mu$. 23. Organe glandulaire sternite 3, $e = 250 \mu$. 24. Organe glandulaire médian de la φ , $e = 44 \mu$. 25. Uro-

peu saillant. *Angles latéraux postérieurs des tergites* : nuls du 1^{er} au 6^e tergites ; en pointe au 7^e où ils se présentent sous forme d'un appendice paraissant articulé sur le tergite ; ceux de la ♀ sont plus cylindriques, plus allongés que ceux du ♂. Au 8^e tergite, les angles sont en pointe aiguë, courte, arquée vers le plan sagittal.

Sternite 1 : préscutum, 4 + 4 *M* longs et 2 + 2 soies courtes ou assez courtes ; scutum, 12 + 12 *M* (*B*₅ nuls), environ 15 + 2 + 15 soies assez courtes ou courtes ; une soixantaine de soies à embase circulaire caractéristique, formant 2 rangées très irrégulières en avant des organes glandulaires postérieurs.

Organes subcoxaux latéraux occupant chacun environ le 1/3 de la largeur inter-styloire. 15 à 18 soies glandulaires dans les 2 sexes, de tailles très inégales ; les plus



Scottojapyx simienensis, gen. et sp. nov., ♂. 26. Papille génitale, l'aire postérieure de soies courtes n'a pas été entièrement représentée, $e = 44 \mu$. 27. Orifice génital vue par l'intérieur de la papille ; *a* = emplacement des appendices génitaux ; *b* = aire postérieure de soies courtes précédée des 7 soies sans embases bordant le bord postérieur de l'orifice génital ; *c* = soies sans embases situées en avant de l'orifice génital ; *d* = ouverture de la cavité qui porte sur sa face tergale les soies sans embases représentées en *c* ; $e = 44 \mu$;

longues, au nombre de 4–5, valent les 39–54/100 de la longueur de st_1 ; les plus courtes, au nombre de 7–11, égalent les 12–16/100 de ce même style ; enfin 2–4 soies de tailles intermédiaires en sont les 20–24/100. L'appareil glandulaire n'a pu être observé. 10–12 soies sensorielles subégales, valant en moyenne les 20/100 de la longueur de st_1 .

Organe glandulaire médian bien développé, peu saillant. Son opercule porte 2 soies courtes sur sa ligne d'articulation et 6 soies extrêmement courtes vers son bord

libre. Chez la ♀, j'ai pu suivre de fins tractus réfringents partant de chacune de ces 6 soies et allant se perdre dans la masse glandulaire antérieure ; je ne saurais cependant affirmer que ce sont des canaux glandulaires. La membrane ne montre aucun orifice glandulaire décelable.

Sternites 2 à 7 : 16 + 16 *M* différenciés ; *B*₄ et les *C* de rang pair indifférenciés, courts ; environ 12 + 2 + 12 soies courtes.

Styles assez allongés, peu épais ; cône secondaire très petit, arrondi ; pore énigmatique bien visible ; $st_1/st_7 = 0,86$; $s_1/s_7 = 1,16$; $s_1/st_1 = 0,19$; $s_1/st_7 = 0,16$.

Vésicules exsertiles petites, présentes du 1^{er} au 7^e sternite

Papille génitale ♂ peu pileuse. Une vingtaine de soies très longues ou longues forment une couronne sur la partie proximale de la base. Les soies courtes de l'aire antérieure sont au nombre de 14. En arrière de ces soies, la membrane s'est invaginée et forme une cavité sensiblement aussi large que profonde, dont l'ouverture est limitée tergalement par le bord de l'orifice génital et sternalement par l'aire antérieure ; cette poche porte sur sa face tergale des soies sans embase, plurisériées, disposées en fer à cheval. Les soies courtes de l'aire postérieure ont leurs embases contiguës près de l'orifice génital, puis s'espacent et s'allongent vers l'extrémité distale de la papille ; elles sont précédées par 7 soies sans embases, insérées tout près du bord de l'orifice génital. Appendices génitaux entièrement membraneux, courts, peu sail-lants, portant chacun une dizaine de soies de toutes tailles, en particulier une soie très courte près de l'apex.

Longueurs relatives des segments 7 à 10 : 49-58-24-100.

CERQUES. Marges internes rectilignes, sans dents ; ils sont peu arqués, mais aigus. Ceux du ♂ égalent les 79/100 de la partie normalement découverte du tergite 10 et sont 2 fois 8/20 aussi longs que larges à la base. La marge interne droite porte 1/12 denticules, le supérieur, situé au niveau du 3^e inférieur, est aigu ainsi que les trois inférieurs proximaux. La marge interne gauche montre 12 denticules, dont les proximaux sont aigus, alors que les autres sont arrondis et de moins en moins nets en allant vers l'apex du cerque.

Ceux de la ♀ égalent les 88/100 de la partie normalement découverte du tergite 10 et sont 2 fois 11/20 aussi longs que larges à la base. La marge interne droite porte 2/12-13 denticules, les supérieurs respectivement au niveau des 3^e et 6^e inférieurs. La marge interne gauche montre 13 denticules dont le 6^e m'a paru être placé sur un plan supérieur à celui des autres. Aux deux cerques, les denticules proximaux sont aigus, les autres arrondis et moins distincts vers l'apex des cerques.

Longueur des spécimens : ♂ 6.5, ♀ 7 mm.

ÉTHIOPIE : Simien, près de Mindigabsa, à une altitude supérieure à 10,000 pieds, 27 Décembre 1952, 1 ♂ et 1 ♀ dans l'humus sous des buissons (*Scott*).

AFFINITÉS : cette espèce est immédiatement reconnaissable à la forme des angles latéraux postérieurs du 7^e urotergite, ainsi que par la forme et l'armature de ses cerques.

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SILVESTRI, F. 1948. Contributo alla conoscenza degli Japygidae (Insecta Diplura). *Rend. dell' Acad. dei XL* (3) 27, 3-115.*

*[This periodical, not easily found in libraries, and liable to be confused with others, is produced by the *Società italiana delle Scienze, detta Accademia dei XL* ("called the Academy of the Forty"). Hence the abbreviation *Rendiconti dell' Accademia dei XL*.—H. S.]

ANTHICIDAE (COLEOPTERA) FROM THE HIGH SIMIEN DISTRICT,
NORTHERN ETHIOPIA. By C. N. HAWKINS, F.R.E.S. (Communicated by
HUGH SCOTT, Sc.D., F.R.S., F.L.S.)

(With 1 text-figure.)

[Read 20 January 1955.]

Two species were collected by Dr. Hugh Scott, between November 1952 and January 1953, in the high Simien, which includes the greatest altitudes in Ethiopia, the highest point, Ras Degien, reaching 15,154 feet. The specimens of *Endomia picina*, described below as new, were found at two of the highest collecting-places visited, respectively 11,500 and 13,200 feet. A single example of a second species, from a more moderate altitude, 7,000 feet, is referred with some reservation to the widely distributed *Endomia unifasciata* Bon.

A record of *Anthicus debilis* Laf., found abundantly on the shore at Jidda, Sa'udi Arabia, during the outward voyage, is added.

The *type* and paratypes of the new species, and examples of the other species, are in the British Museum.

The Anthicidae collected by Dr. Hugh Scott and Professor J. Omer-Cooper in Ethiopia (Abyssinia) in 1926-27, and by Dr. Scott in Southern Ethiopia in 1948-49, were the subject of a paper by M. Maurice Pic in 1951 (*Ann. Mag. Nat. Hist.* (12), 4, 126-36). M. Pic enumerated some 20 forms, among which the genera *Notoxus*, *Formicomus*, *Tomoderus*, *Anthicus*, *Aulacoderus* and *Endomia* are represented: one species of *Notoxus* and five of *Anthicus* being described as new. There was, however, only one *Endomia*, which he constituted a new variety of *E. minuta* Pic, a species originally based on specimens from West Africa, and very different from the new species described below. The genus *Endomia* has a wide range, including southern Europe, western Asia, the Oriental Region, Africa and Madagascar.

(A Correction: in the paper by M. Pic cited above, the data as to where *Endomia minuta* var. *scotti* was found were omitted: they should read "near the Catar (or Kattere) River, east of Lake Zwai, c. 6,000 ft., 6. xi. 1926, 1 ex. (Scott)").

ENDOMIA Cast.

Endomia picina, sp. n.

Size slightly larger than average *Endomia unifasciata* Bon., i.e. about 3 mm. in length. Winged. Colour dark pitchy, with the legs and lateral borders of the elytra paler: antennae, palpi and mouth-parts almost ferruginous, with the club of the antennae slightly darker: joint 2 of antennae shorter and joints 4 and 5 each somewhat longer than the individual joints 3 and 6 to 11, which latter thicken gradually to form a slender club. Punctuation of head, thorax and elytra strong and fairly evenly but not very closely or regularly spaced (i.e. not in straight longitudinal or transverse rows), with the intervals polished, giving the whole insect a shiny appearance. There is some indication of very fine reticulation on some parts, particularly at the edges of the punctures. Each puncture on head, thorax and elytra gives rise to a slender hair-like scale, which is strongly curved backwards and is long enough to reach at least to and often beyond the next puncture. These hair-like scales appear pale golden. There are similar hair-scales on the legs rising from finer punctures, but these, by artificial light, seem to be white.



Endomia picina, sp. n.

ETHIOPIA : Simien : Mai Datcha (east of Arcuasié), c. 13,200 ft., 5. xii. 1952, *holotype* taken from litter in tunnels of small rodents, and two paratypes taken from marshy floor of valley ; Lori, 11,500 ft., 29-30. xi. 1952, one paratype taken at night on floor of lighted tent (all *Scott*).

Endomia unifasciata Bon. (?).

ETHIOPIA : Simien : near Dabat, from valley south of the Falasha Mission, c. 7,000 ft., 21. i. 1953, 1 ex. (*Scott*).

This species was described from Southern Europe, and is known from North Africa and parts of Asia. The specimen recorded above is provisionally referred to *E. unifasciata*, of which it is probably a varietal form.

ANTHICUS Payk.

Anthicus debilis Laf.

SA'UDI ARABIA : Jidda, from debris on the shore near the jetty, 2-3. x. 1952, 36 ex. (*Scott*).

This species is widely distributed in Mediterranean lands. Egypt, Eritrea, Arabia, etc. The specimens here recorded were collected while the ship lay at Jidda on the outward voyage to Massawa. That so many were obtained during two short periods of collecting in seaweed and other shore-debris is an indication of their local abundance.

JOURNEY TO THE GUGHÉ HIGHLANDS (SOUTHERN ETHIOPIA), 1948-49 : COLEOPTERA, PSEPHENIDAE ; THE IMMATURE STAGES OF EUBRIANAX SCOTTI PIC. By C. E. DYTE, Department of Zoology, University of Bristol. (Communicated by HUGH SCOTT, Sc.D., F.R.S., F.L.S.)

(With figures 1-3.)

[Read 21 October 1954.]

This description is based on larvae, larval skins from pupal cases, and pupae of *Eubrianax scotti* Pic (1953) collected with the adults from wet grit and stones in a river bed about two miles south of the town of Dilla. Sidamo Province, Abyssinia, about 5,100 feet, 20. i. 1949.

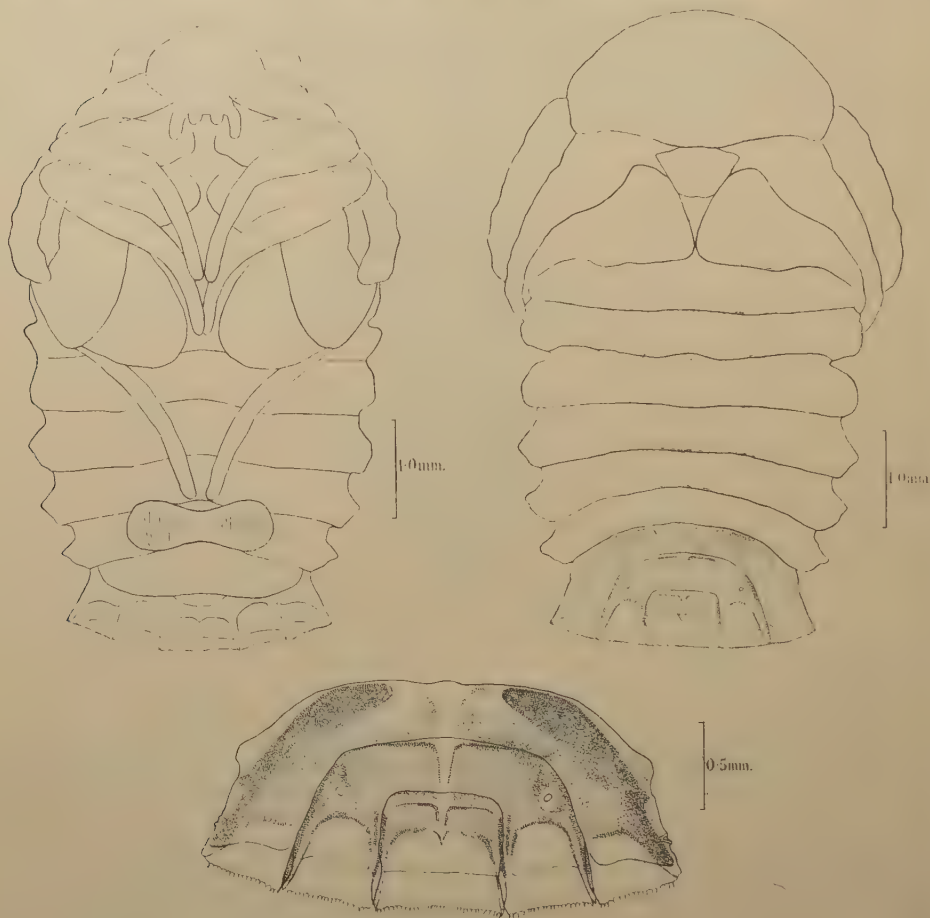
Larvae : these appear to be identical with those previously collected in Abyssinia by Dr. Hugh Scott, which were described by Hinton (1940), before the adult was known.* The larval skins from pupal cases consist of the dorsum of the mature larva with the exception of abdominal segments seven to nine, which are replaced by the posterior part of the pupa. These skins are of two sizes, 6.6 mm. (average of seven specimens varying from 6.0 mm. to 7.5 mm.) and 9.6 mm. (average of five specimens varying from 9.5 mm. to 10.0 mm.); this size difference is to be expected from a similar difference in the adult beetles, the male and female illustrated by Pic being 5.5 and 8.4 mm. long respectively. In the four complete larvae examined, the length to the apex of the sixth abdominal tergite averages thirteen-fifteenths of the total length, so that the length of the mature larvae of the male will be about 7.6 mm., and of the female 11.1 mm.

Pupae : the pupal material consists of one male and three female pupae, with a single male pupal exuvium. The dorsal and ventral aspects of the pupa with larval skin detached are shown in figs. 1-2. Besides a difference in size (male 5.5 to 6.0 mm., female 8.5 to 9.0 mm.), in the female pupa the antennal sheath reaches only to the most lateral part of the second leg sheath, whereas in the male the end of the proportionately longer antennal sheath lies beyond this under the elytral sheath (fig. 1). In both sexes there is a dumb-bell shaped organ of attachment on the ventral side of the sixth abdominal segment. The basal parts of the second and third leg sheaths are separated by the apices of the elytral and wing sheaths, which are folded round the body to the ventral side.

The dorsal surface, with the exception of the posterior part, which replaces segments 7 to 9 of the larval dorsum, is entirely membranous. The 'scuta abdominaux bruns' of Bertrand (1935) would appear, at least in this species, to be dark areas of the pharate adult showing through the membranous pupal cuticle. They are not present in less mature specimens.

*[A word of explanation may be added here. Monsieur Pic's description of this species was, as stated above, based on the series of adult beetles which I collected near Dilla in Sidamo Province, far south of Addis Ababa, in January 1949; and Mr. Dyte's descriptions of the early stages are based on material found at the same time and place with these adults. But I had previously, in December 1926, collected three adult specimens in the Muger Valley, over 30 miles north of Addis Ababa. These were overlooked until after Monsieur Pic's description was drawn up, when they were identified by Mr. C. N. Hawkins. *Eubrianax scotti* is thus known to occur in these two places, some 200 miles apart in an approximately north and south direction; but in both cases at only moderate altitudes, about 5,100 feet near Dilla, and 5,500 feet in the Muger Valley. If, however, the two larvae described (without pupae or adults) by Dr. Hinton in 1940 as '*Eubrianax* sp.' are really of the same species, then its range in altitude is greater, for these two were found at about 8,500 ft. in the valley of the Douber, an upper tributary of the Muger.—HUGH SCOTT.]

The pupae of only two other species of *Eubrianax* are known. That of *E. edwardsi* (Lec.) has been described by Blackwelder (1930) and figured by Essig (1926). Bertrand



FIGS. 1-3.—Male pupa of *Eubrianax scotti* Pic.

(1) Ventral view. (2) Dorsal view. (3) Dorsal view of posterior sclerotized part.

(1935) has illustrated the pupa of one species (probably *E. major* Pic) from the East Indies.

I wish to thank Dr. H. E. Hinton for his help in writing this note.

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JOURNEY TO THE HIGH SIMIEN (NORTHERN ETHIOPIA), 1952-3 THREE: SPECIES OF PHENACOLIMAX (GASTROPODA, VITRINIDAE), WITH NOTES ON THE TAXONOMY OF THE GENUS. By Dr. Lothar Forcart, Museum of Natural History, Basle, Switzerland. (Communicated by Hugh Scott, Sc.D., F.R.S., F.L.S.)

(With Plate 4 and 3 Text-figures.)

[Read 21 October 1954.]

INTRODUCTION.

Dr. H. E. Quick, on behalf of Dr. W. J. Rees of the British Museum (Natural History), kindly entrusted me with the examination of the Vitrinidae which Dr. Hugh Scott collected in 1952 on his journey to the High Simien in Northern Ethiopia (Abyssinia).

Connolly (1928, 178-179) included 24 species and 2 subspecies of *Vitrina* and 2 species of *Granularion*, the latter described originally under *Vitrina*, in his list of the Molluscan Fauna of Abyssinia. A revision of those species, most of them insufficiently described and poorly figured, is very necessary, and would probably reduce the number of species. I have been able to revise some of those species by comparison with their type specimens.

ACKNOWLEDGEMENTS.

I am greatly indebted to Dr. H. E. Quick for comparing the shells of the species collected by Dr. Hugh Scott with the lectotypes and paratypes of *Vitrina abyssinica* Pfeiffer, 1848; *Vitrina rüppelliana* Pfeiffer, 1848; *Vitrina hians* Pfeiffer, 1848; *Vitrina darnaudi* Pfeiffer, 1856; and *Vitrina sennariensis* Pfeiffer, 1856 in the Cuming Collection in the British Museum (Natural History). To Dr. A. Franc, subdirector of the laboratory of malacology at the National Museum of Natural History, in Paris, I am indebted for the loan of the syntypes of *Vitrina raffrayi* Bourguinat, 1883; and to Dr. A. Zilch, curator at the Natur-Museum Senckenberg, Frankfurt a. Main, for the loan of the rich collection of Vitrinidae from Abyssinia in that Museum, containing the lectotype and paratypes of *Vitrina jamjamensis* Kobelt, 1905, and paratypes of *Vitrina deverei* Jickeli, 1873, and *Vitrina planulata* Jickeli.

I wish to express my best thanks also to Dr. G. Mermod, Curator at the Museum of Natural History at Geneva, for the loan of publications and to O. Garraux of Basle for the execution of the figures.

I. PHYLOGENY AND TAXONOMY.

The vagina of the species of *Phenacolimax*, *Arabicitrina*, *Oligolimax*, *Insulivitrina*, and *Plutonina* differs in its anatomy and function from that of all other Vitrinidae. It is composed of a proximal* and a distal part. The distal part forms an acorn-shaped papilla or *glans*, which enters the proximal part of the vagina by a conical spout. It has muscular walls with interior and often also exterior coats of glandular tissue. The oviduct and the spermatheca enter the distal end of the vaginal papilla (cf. Boycott, 1922, 128, fig. 4).

* The terms 'proximal' and 'distal', in the case of the genital organs, are related to the genital orifice in the epidermis, taken as the base of orientation. The parts of the organs, situated nearer to the genital orifice are characterized as proximal, those situated more distantly as distal.

When protruded, the penis and the vagina become evaginated, as Mermod (1923, 313) presumed. The proximal part of the vagina becomes completely evaginated, so that the spout of the vaginal papilla becomes the distal point of the everted vagina (cf. Forcart, 1949, 115-119, fig. 2). This mode of vaginal eversion is analogous to the penial eversion of the genus *Helix*.

The Vitrinid genus *Semilimax* has an accessory organ which, in addition to the penis and the vagina, enters the atrium. This organ is composed of a glandular part and an excretory tube, which consists of conchyolin. Simroth (1886, 6-7) considered this excretory tube to be homologous with the dart of the genus *Helix*, and (Simroth, 1888, 40-43 and 1889, 35-36) named the glandular part 'Pfeildrüse' and the excretory tube 'Liebespfeil'. In those publications he considered the accessory gland of *Semilimax* to be homologous with the vaginal papilla of *Insulivitrina* and *Phenacolimax*.

Simroth (1889, 39) put forward the theory that those Vitrinidae with an accessory organ are the most primitive group of the family, from which those possessing a vaginal papilla arose by transference of the accessory organ to the vagina; while the group without either accessory organ or vaginal papilla originated through loss of these organs.

Wiegmann (1886, 75) rejected Simroth's theory that the accessory organ of *Semilimax* is homologous with the dart gland of *Helix*, and stated that the muscular acorn-shaped part or *glans* in the vagina of *Insulivitrina* and the accessory organ of *Semilimax* are different organs, since neither their structure nor their situation give any grounds for the hypothesis that they are homologous.

Eckhardt (1914, 367), in his profound study of the Vitrinidae of Germany, rejected Simroth's theory that *Vitrina pellucida* and *Eucobresia diaphana* are descendants of a form with an accessory organ. He concluded from his studies that the Vitrinidae with an accessory organ and those without such an organ are of diphyletic origin.

Boycott (1922, 130) concluded from his studies on *Phenacolimax major* that Simroth's theory, namely that the accessory organ of *Semilimax* is homologous with the dart gland of *Helix*, 'is at best a dubious speculation, functionally it is impossible'.

Hesse (1923, 81) accepted Simroth's theory that the muscular glans of the vagina in *Phenacolimax major* and the accessory organ of *Semilimax* are homologous, but rejected the theory that those organs are homologous with the dart gland of *Helix*. Consequently he changed Simroth's expression 'Pfeilsack' (=dart gland) of the Vitrinidae to 'Liebesdrüse' (=love gland). He proposed the following taxonomy for Vitrinidae with a vaginal papilla:

To *Phenacolimax* (which he named incorrectly *Vitrina*) and *Insulivitrina* he gave the rank of genera.

Oligolimax and *Gallandia*, of which he did not know the anatomy of the genital organs, he regarded as subgenera of *Vitrina* (which he named incorrectly *Phenacolimax*).

Vitrina arabica Thiele, the type species of *Arabivitrina* Thiele, 1931, he considered as a species of the genus *Insulivitrina*.

Baker (1929, 139), revising the nomenclature of the Vitrinidae, united all Vitrinidae in the genus *Vitrina*. He considered Hesse's genera as subgenera, and Hesse's subgenera as sections.

Thiele (1931, 599-600) accepted Baker's taxonomy. He proposed *Arabivitrina*, with *Vitrina arabica* Thiele as type-species, as a section of the subgenus *Insulivitrina*. He added the genus *Plutonia* to the family Vitrinidae, but separated it from the other Vitrinidae as a subfamily Plutoniinae.

Forcart (1944) considered *Phenacolimax*, *Insulivitrina*, and *Oligolimax* as different genera, and recognized *Gallandia* as synonymous with *Oligolimax*.

Forcart (1949) described the eversion of the penis and vagina of *Phenacolimax major*, and classified the Vitrinidae with regard to their different modes of copulation.

He showed (p. 118) that the species of *Phenacolimax*, *Oligolimax*, and *Insulivitrina* have an erectile vagina, and that those species and *Vitrinobrachium breve* (Férussac) copulate without internal coitus, exchanging the sperm exteriorly like the Limacidae. The species of *Vitrina*, *Eucobresia*, and *Semilimax* copulate by means of internal coitus.

Hubendick (1953, 90-95) considered *Phenacolimax* as a subgenus of *Vitrina*, and *Insulivitrina* and *Arabivitrina* as synonymous with *Phenacolimax*. He supposed that *Oligolimax* belongs probably to the group of *Semilimax*, which he named incorrectly *Vitrinopugio*. He wrote that he came to this conclusion 'according to Mermod's (1923, 1927) description of the genitalia of *Vitrina annularis* Stud.'. But the descriptions and figures of Mermod (1923, 310-313, fig. 2 and 1927, 332-336, pl. 16, fig. 1) show clearly that *Oligolimax* belongs to the group of *Phenacolimax*. Mermod's descriptions have been confirmed by examination of specimens of *Oligolimax annul. ris* from France, Switzerland, and Anatolia.

Hubendick (1953, 84, 95, fig. 21 on p. 88) described a callosity which he observed on the wall of the vagina of *Vitrina lactea* Connolly from Mt. Kenya as consisting of glandular tissue. He concluded (p. 95) from this observation: 'The evolution of a comparatively distinct gland in the wall of the vagina may indicate a possible clue to the origin of *Phenacolimax*, where the vagina is particularly well developed'. This callosity is probably a pathological tumour without any phylogenetic importance. I observed a similar callosity on the uterus of a specimen of *Helicigona achates raetica* (Strobel) from the Valteline. The histological examination proved its pathological nature.

Simroth (1891, 223-229, pl. 1, figs. 1-13) examined the anatomy of *Plutonia atlantica* (Morelet), an Azorean species resembling *Testacella* in its exterior appearance and its biology, and concluded that *Plutonia* is a specialized descendant of *Insulivitrina*.

We may conclude that the Vitrinidae which have an erectile vagina with a muscular papilla are descendants of a common stock, and that no forms intermediate between them and the other groups of Vitrinidae are known.

The species of *Oligolimax*, with their relatively well-developed shell and their primitive mantle, are probably the most primitive forms of this group.

Insulivitrina, *Arabivitrina*, and *Phenacolimax* developed, probably independently of each other, from an ancestral form, of which *Oligolimax* represents a less specialized descendant.

Plutonia is probably a specialized descendant of the ancestral stock, of which *Insulivitrina* is a less specialized descendant.

If this hypothesis is correct, *Oligolimax*, *Insulivitrina* and *Plutonia* are representatives of three successive evolutionary stages, all living at the present time.*

Consequently the Vitrinidae with an erectile vagina, which has a muscular distal papilla, are taxonomically arranged as follows:

Genus PHENACOLIMAX Stabile.

Phenacolimax Stabile, 1859, *Rev. Mag. Zool. Guérin Paris*, (2) 11, 422. Type-species: *Phenacolimax* (*Phenacolimax*) *major* (Férussac) = *Helico-limax major* Férussac, 1807. Type designation: Fischer in Paulucci, 1878, *Faune malac. Italie*, 24.

* Since this paper was submitted for publication, N. H. ODHNER (1954, *Proc. Malac. Soc. Lond.*, 31 (2), 56-63, pl. 4) has described the morphology and anatomy of *Helix cuticula* Shuttleworth, 1852, native of the Canary Islands. Though all its organs agree closely with those of *Phenacolimax*, Odhner makes it the type-species of a new subgenus, *Guerrina*, which he places in *Vitrina*. But according to my definition of the characters and probable relationships of the genera, given above, *Guerrina* should be a subgenus of *Phenacolimax*, not of *Vitrina*.

Guerrina is probably a representative of the same evolutionary stage as *Oligolimax*. Both subgenera developed from an unknown ancestral stock by divergent evolution. The genital organs of the subgenera *Insulivitrina*, *Arabivitrina*, and *Phenacolimax* show closer agreement with those of *Guerrina* than with those of *Oligolimax*, so that we must conclude that *Guerrina* represents a form closer related to the ancestral stock of these subgenera, than does *Oligolimax*.

Vitrina Hesse, 1923, nec Draparnaud, 1801; *Arch. Moll.* **55** (3), 82. Type-species by designation: *Vitrina pellucida* Draparnaud, 1801 = misidentification of *Phenacolinax* (*Phenacolinax*) *major* (Férussac), not *Vitrina pellucida* (Müller). By Opinion 119, rendered 1931 by the Intern. Comm. Zool. Nomencl., *Vitrina* Draparnaud, 1801, with *Helix pellucida* Müller, 1774 as type-species, was placed in the Official List of Generic Names.

Subgenus OLIGOLIMAX Fischer.

Oligolimax Fischer, 1878 in Paullucci, *Faune Malac. Italie*, 1, 2. Type-species by original designation: *Phenacolinax* (*Oligolimax*) *pauvucciae* (Fischer) = *Vitrina pauvucciae* Fischer, 1878.

Gallandia Bourguinat, 1880, *Descr. nouv. genre Gallandia*. Type-species by original designation: *Vitrina conoidea* Martens, 1874 = synonym of *Phenacolinax* (*Oligolimax*) *annularis* (Studer).

Diagnosis: the vagina has a short proximal and a longer distal part. The distal half of the latter is covered by glandular tissue. The penis is much shorter than the vagina. The atrium is elongated.

The mantle does not cover the shell. Its dorsal body-lobe and left shell-lobe are short.

The shell is globose, and has more than three whorls. The last whorl is not extraordinarily enlarged towards the aperture. The surface of the protoconch and the other whorls is radially striate.

DISTRIBUTION: Alps, mountains of southern Europe, Caucasus, highlands of Anatolia, Iran, and Turkestan.

Subgenus ARABIVITRINA Thiele.

Arabivitrina Thiele, 1931; *Handbuch syst. Mollusken-Kunde*, 2, 600. Type-species as monotype: *Phenacolinax* (*Arabivitrina*) *arabica* (Thiele) = *Vitrina arabica* Thiele, 1910.

Diagnosis: the proximal and the distal parts of the vagina are approximately equal in length. The penis is about as long as the vagina. It contains a strong, longitudinal torus of glandular tissue, which swells up on the everted penis. The atrium is elongated.

The right shell-lobe of the mantle differs in length in different species: in some it covers only the anterior border of the shell, in others it reaches to the middle of the shell.

The shell is composed of less than three whorls, of which the last is enlarged towards the aperture. The surface of the protoconch is micro-punctate or smooth, that of the other whorls more or less distinctly wrinkled.

DISTRIBUTION: Highlands of South-west Arabia, Abyssinia, Kenya, and Uganda.

Subgenus PHENACOLIMAX, s. str.

Diagnosis: the vagina is as in the subgenus *Arabivitrina*. Its distal part is wrapped in glandular tissue (in *Phenacolinax stabilei*) or covered by two glandular lobes (in *Phenacolinax major*). The penis is as in the subgenus *Arabivitrina*. The vagina and the penis join immediately before the genital orifice, so that the atrium is very short.

The right shell-lobe of the mantle reaches to the middle of the shell.

The shell has $2\frac{3}{4}$ to $3\frac{1}{4}$ whorls. The surface of the protoconch is micro-punctate.

DISTRIBUTION: Western and South-western Europe.

Subgenus INSULIVITRINA Hesse.

Insulivitrina Hesse, 1923, *Arch. Moll.*, **55** (4), 131. Type-species: *Phenacolinax* (*Insulivitrina*) *lamarckii* (Férussac) = *Helicolimax lamarckii* Férussac, 1821. Type designation: Hesse, 1924, *Arch. Moll.*, **56** (6), 226.

Diagnosis: the proximal and the distal part of the vagina are exteriorly not differentiated. The vagina has no exterior glandular tissue. The penis is shorter than the vagina; in some species it is as small as in the genus *Oligolimax*. The atrium is elongated in the species inhabiting the Atlantic Islands and short in the alpine *Phenacolinax* (*Insulivitrina*) *glacialis* (Forbes).

The right shell-lobe of the mantle covers the greater part of the shell.

The shell has $1\frac{1}{2}$ to $2\frac{1}{2}$ whorls, of which the last is enlarged. The protoconch is micro-punctate.

DISTRIBUTION : Atlantic Islands and high Alps, above the upper tree-limit.

Subgenus PLUTONIA Stabile.

Plutonia Stabile, 1864, *Atti Soc. Sci. Nat. Milano*, 7, 121. Type-species as monotype : *Phenacolinax* (*Plutonia*) *atlantica* (Morelet) = *Viquesnelia atlantica* Morelet, 1860.

Vitriplutonia Collinge, 1893, *Conchologist*, 2, 204. Nom. nov. for *Plutonia* Stabile, 1864.

Diagnosis : the genitalia do not differ from those of the subgenus *Insulivitrina*. According to Simroth (1891, 228) the retractor muscle of the penis is missing.

The shell is small, flat, and analogous to that of *Limax* : it is completely overgrown by the mantle. The body behind the mantle is keeled.

DISTRIBUTION : Azorean archipelago.

BIOLOGY : a subterranean-living group : the species feed on worms, as in *Testacella* and *Daudebardia*.

II. SPECIES COLLECTED BY DR. HUGH SCOTT.

Dr. Hugh Scott collected all the following species on his caravan journey in the High Simien, in Northern Ethiopia (Abyssinia). The expedition left Debarec, on the motor road from Adua to Gondar, on 15 November 1952, traversed the massif of Ambaras, passed over the gigantic northern precipice of Mt. Buahit, and arrived on 8 December at the foot of Ras Degien, about 34 miles east of Debarec. I am greatly indebted to him for information about his expedition and for the loan of a photograph of a map of his route, the original of which he will publish later.

Phenacolinax (*Arabivitrina*) *abyssinicus* (Pfeiffer). (Pl. 4, figs. 1 a-d, 4.)

Vitrina abyssinica [Rüppell] Pfeiffer, 1848, *Proc. Zool. Soc. London*, 16, 108. Lectotype and 1 paratype in the British Museum (Cuming Collection) from Abyssinia, collected by Dr. E. Rüppell 1832-1833* ; Reeve, 1862, *Conch. Ic.*, 13, *Vitrina*, pl. 9, fig. 61.

? *Vitrina helicoidea* Jickeli, 1873, *Malac. Bl.*, 20, 99. Type not known. Type-locality : Eritrea, between Ghinda and Asmara, collected by C. F. Jickeli, 1871† ; Jickeli, 1874, *Nov. Acta Acad. Leop.*, 37 (1), 43, pl. 4, fig. 2.

Material : 7 specimens (4 in Brit. Mus. and 3 in Mus. Basle 5811-a), from Aostagheb, 11,500 ft., on the south slope of Ambaras, a long massif running in the direction E.S.E. to W.S.W., and about 20 miles west of Ras Degien. At roots of grass with *Phenacolinax darnaudi*, 21. xi. 1952.

TAXONOMY : Dr. H. E. Quick compared a shell with the lectotype and paratype of *Phenacolinax abyssinicus* in the British Museum, and found it identical.

Three shells in the Senckenberg Museum (No. 120340), collected by Dr. E. Rüppell and determined as *Vitrina* (*Arabivitrina*) *helicoidea* Jickeli, are identical with the shells from Aostagheb. Probably they belong to the original lot of *Phenacolinax abyssinicus*. *Vitrina helicoidea* Jickeli is, as far as can be concluded from the description and figures in Jickeli (1874, pl. 4, fig. 12), synonymous with *Phenacolinax abyssinicus* (Pfeiffer).

A damaged shell in the Senckenberg Museum, marked as a paratype of *Vitrina* (*Arabivitrina*) *abyssinica* (Pfeiffer) (No. 8623) and collected by Rüppell, is a specimen of *Vitrina rüppelliana* Pfeiffer.

* Dr. E. Rüppell travelled from Massaua to Gondar, passing through the province of Tigré and the district of Simien. I select High Simien as the restricted type locality of *Phenacolinax abyssinicus*.

† [Asmara stands at about 7,400 feet, near the eastern edge of the Eritrean high plateau ; Ghinda lies at about 2,670 feet, in the foot-hills to the north-east, roughly one-third of the way down to the Red Sea coast. The record of Jickeli's specimen, as quoted by Dr. Forcart, includes the term 'province of Amasan' ; but the name Hamasen (to give the more usual orthography) is generally applied to the high plateaux west and south-west of Asmara rather than to the country east of that city.—HUGH SCOTT.]

Shell (Pl. 4, figs. 1 *a-d*, 4) : the shell is depressed, almost flat. The protoconch has one whorl, and a smooth, convex surface. The rest of the whorls rapidly enlarge, their surface is slightly wrinkled, and at their beginning less convex than the protoconch. The body-whorl is at the aperture more than three times as large as the penultimate whorl. 4.3 mm. : 1.3 mm., in the figured shell from Aostagheb, which probably is not fully grown.

Largest diameter 8 mm., smallest diameter 6 mm., altitude 5.3 mm., diameter of the aperture 5 mm., altitude of the aperture 5.4 mm., $2\frac{1}{4}$ whorls.

Mantle (Pl. 4, fig. 4) : the left body-lobe is large, and reaches the head. Both shell-lobes are small, and cover the shell only near the aperture.

Colouring : the animals, having been preserved in alcohol, are yellowish grey with dark longitudinal bands and dark spots. The body is, on the peripodial zone, more darkly pigmented. The body-lobes of the mantle have dark spots and a dark longitudinal band, which runs on the right side over the respiratory orifice. The part of the mantle covered by the shell has dark bands and spots, which shine through the shell. All the bands and spots of the mantle show individual variations, and are in some specimens only little developed.

Genitalia (fig. 1) : all the specimens examined are juvenile. The atrium is elongated. The vaginal papilla projects by an obtuse spout into the proximal

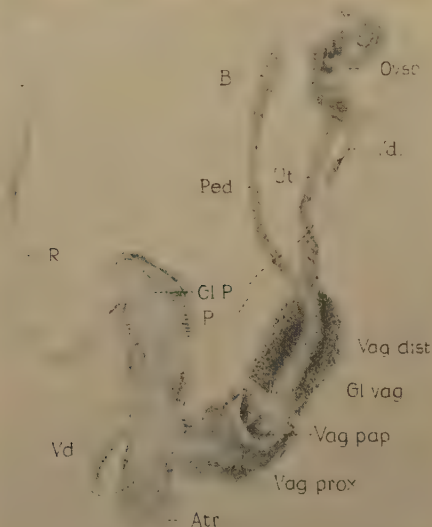


FIG. 1.—Genitalia of *Phenacolimax* (*Arabivitrina*) *abyssinicus* (Pfeiffer). (Mus. Basle 5811-a, prep. VI-18). Atr. = Atrium; B. = bursa of the spermatheca; Dh. = hermaphrodite duct; Gl. alb. = albumen gland; G.P. = penial glandular torus; Gl. Vag. = vaginal glandular tissue; Ovisp. = ovispermiduct; P. = penis; Ped. = duct of the spermatheca; R. = penial retractor muscle; Ut. = free uterus; Vag. dist. = distal part of the vagina; Vag. pap. = vaginal papilla; Vag. prox. = proximal part of the vagina; Vd. = vas deferens.

vagina. The proximal vagina is stout and covered by glandular tissue, but not by glandular lobes as in the subgenus *Phenacolimax*, s. str. The proximal and the distal parts of the vagina are of equal length. The spermatheca has a long duct and a bursa, of about the same diameter as the duct, which is a juvenile feature.

The penis has about the same length as the vagina. Its glandular spongy tissue has on its central part peculiar transverse folds. The retractor muscle is inserted near the distal end of the penis. The vas deferens enters the central part of the penis.

Mandible: the mandible is oxygnath and carinated in its middle. This median keel terminates on the cutting margin in a pointed projection.

Radula: the teeth of the radula are formed as those of *Phenacolimax major*, as described by Hesse (1923, 15-18, pl. 1, fig. 7): that is, the marginal teeth have rudimentary ectocones, not well developed ectocones as Thiele (1910, pl. 10, fig. 7) figured for *Phenacolimax (Arabivitrina) arabica* (Thiele).

The teeth of some species of *Phenacolimax* show a considerable amount of variability, as is evident from the descriptions given by Mermod (1923, 310-312, fig. 1; 315-316, fig. 8; and 1927, 335-336, pl. 16, fig. 2) of the radula of *Phenacolimax (Oligolimax) annularis* (Studer), partly described as *Phenacolimax conoidea* (Martens), and by Bowell (1927, 145-146, pl. 11, figs. 2-3) of the radula of *Phenacolimax major*.

Phenacolimax (Arabivitrina) darnaudi (Pfeiffer). (Pl. 4, figs. 2 a-d, 5).

Vitrina darnaudi Pfeiffer, 1856, *Proc. Zool. Soc. London*, **24**, 325. Lectotype and 2 paratypes in the British Museum (Cuming Collection) from "Sennaar" *), collected by d'Arnaud; Pfeiffer, 1858, *Nor. Conch.*, **1**, 101, pl. 28, figs. 19-21, Reeve, 1862, *Conch. Ic.*, **13**, *Vitrina*, pl. 5, figs. 32 a-b.

Material: 7 specimens (4 in Brit. Mus. and 3 in Mus. Basle, 5812-a) from Aostagheb, found together with *Phenacolimax abyssinicus*.

Shell: Dr. H. E. Quick compared a shell from Aostagheb with the types of *Phenacolimax darnaudi*, and found it to agree, though a little smaller.

The shell (Pl. 4, fig. 2 a-d) differs from that of *Phenacolimax abyssinicus* by its larger dimensions, by the more convex whorls, and the raised spire. A reddish yellow periostracum covers the calcareous shell, and is easily detached from dry shells. The body whorl is at the aperture nearly 2.5 times as large as the penultimate whorl (8 mm.: 3.4 mm.).

Largest diameter 13.4 mm., smallest diameter 10.4 mm., altitude 10.3 mm., diameter of the aperture 8.6 mm., altitude of the aperture 8 mm., 2 $\frac{3}{4}$ whorls.

Mantle: the lobes of the mantle are a little less developed than in *Phenacolimax abyssinicus*.

Colouring: the body and the mantle of specimens preserved in alcohol are greyish, without markings.

Genitalia (fig. 2): the dissected specimens are not fully adult. Their genitalia differ from those of *Phenacolimax abyssinicus* in the form of the vagina, of which the proximal part is nearly twice as long as the distal part, in the absence of the vaginal gland, and the relatively shorter penis which has only about $\frac{2}{3}$ of the length of the vagina. The glandular spongy tissue of the penis runs as a longitudinal fold along the inner wall of the penis, and is distally bent. Its transverse folds are much weaker than in *Phenacolimax abyssinicus*. The retractor muscle is inserted at the distal end of the penis, and the vas deferens enters that organ at its middle.

Mandible and radula: these do not differ from those of *Phenacolimax abyssinicus*.

Phenacolimax (Arabivitrina) riepiana (Jickeli). (Pl. 4, figs. 3 a-d, 6).

Vitrina riepiana Jickeli, 1882; *JB. deutsch. malak. Ges.*, **9**, 366. Situation of type specimen not known (possibly in Museum at Sibiu, formerly Hermannstadt, in Rumania, or elsewhere in that country). Type-locality: province of Amasan (Hannasen) in Eritrea (regarded in 1871 as part of Abyssinia).

[*Vitrina* sp. (?) Connolly, 1928; *Proc. zool. Soc. Lond.*, 165].

Material: Abyssinia; 3 specimens (2 in Brit. Mus. and 1 in Mus. Basle, 5813-a) from Ras Degien, above 14,000 feet, below the 'Pass of Degien', 11. xii. 1952.

* D'Arnaud, a French engineer in Egyptian service, lived from 1840 to 1843 in Sennaar. As the Egyptian troops, to which d'Arnaud was attached, undertook at that time military expeditions to the highlands of northern Abyssinia, the type specimens of *Phenacolimax darnaudi* and other species, collected by d'Arnaud, may be of Abyssinian origin.

Taxonomy: Dr. H. E. Quick, after comparing a shell from Ras Degien with the Abyssinian Vitrinidae in the British Museum, wrote: "*V. ? modesta* Pollonera. The British Museum specimen was collected by J. Omer-Cooper in 1926, in Jem-Jem Forest, west of Addis Ababa. In any case the Ras Degien specimen is not *abyssinica*, *darnaudi*, *hians*, *rüppelliana* or *sennariensis*". The comparison of the specimens from Ras Degien with the original description of *Vitrina modesta* (Pollonera, 1898, 3-4, pl. figs. 10-12) shows that the latter species has a nearer relationship, if it is not synonymous, with *Phenacolinax abyssinicus*.

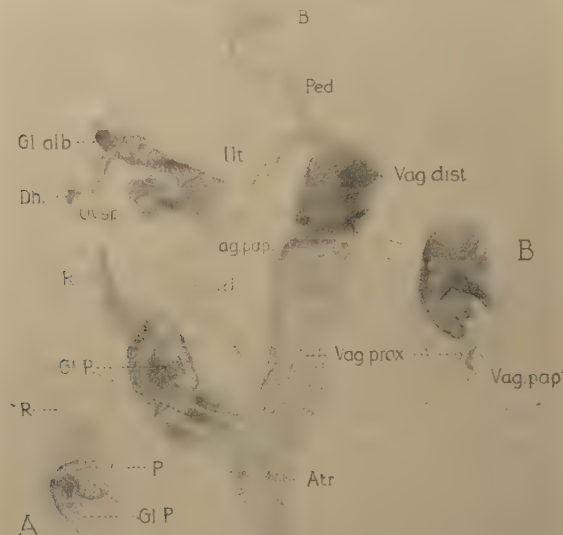


FIG. 2.—Genitalia of *Phenacolinax (Arabivitrina) darnaudi* (Pfeiffer). A, opened distal part of the penis. B, opened distal part of the vagina. Abbreviations as in fig. 1. (Mus. Basle 5812-a, prep. VI-21, VI-22.)

The shell from Ras Degien conforms with the original description of *Vitrina riepiana*.

Shell (Pl. 4, figs. 3 a-d): the shell is depressed, and has no mammillate apex. The protoconch has $1\frac{1}{2}$ whorls, and is spirally micro-punctate. The surface of the whorls is nearly flat and the suture is hardly impressed.

The body-whorl is, at the aperture, 5 times as large as the penultimate whorl (6 mm. : 1.2 mm.).

Largest diameter 9 mm., smallest diameter 6.5 mm., altitude 4.4 mm., diameter of the aperture 5.7 mm., altitude of the aperture 5.2 mm., $2\frac{5}{8}$ whorls.

Mantle (Pl. 4, fig. 6): the left body-lobe is large and covers the head of the extended specimen. The right shell-lobe is tongue-shaped, and covers the greater part of the spire.

Colouring: the preserved specimens are unicolorous bluish-black.* The side areas of the foot are not as dark as the body and the mantle, but darker than the mid-area.

[* The blackness of these specimens struck me very much when I found them. Their colour contrasted strongly with that of all the other examples of *Vitrina* collected on this journey. I wrote in my journal that they were "a cluster of snails under a stone, of ordinary-looking form, but nearly black".—HUGH SCOTT.]



EXPLANATION OF PLATE 4.

- FIG. 1. Shell of *Phenacolimax (Arabivitrina) abyssinicus* (Pfeiffer). 1 a, natural size ; 1 b-d, x 3. (Mus. Basle 5811-a.)
- FIG. 2. Shell of *Phenacolimax (Arabivitrina) darnaudi* (Pfeiffer). 2 a, natural size ; 2 b-d, x 2. (Mus. Basle 5812-a.)
- FIG. 3. Shell of *Phenacolimax (Arabivitrina) riepiana* (Jickeli). 3 a, natural size ; 3 b-d, x 3. (Mus. Basle 5813-a.)
- FIG. 4. *Phenacolimax (Arabivitrina) abyssinicus* (Pfeiffer). x 2. (Brit. Mus.)
- FIG. 5. *Phenacolimax (Arabivitrina) darnaudi* (Pfeiffer) x 2. (Brit. Mus.)
- FIG. 6. *Phenacolimax (Arabivitrina) riepiana* (Jickeli) x 2. (Brit. Mus.)



Genitalia (fig. 3): the dissected specimen is adult, but has probably not yet mated. The atrium is long. The proximal and distal parts of the vagina are about of equal length. The distal part is covered by glandular tissue. The vaginal papilla enters the proximal part of the vagina by a pointed spout. The spermatheca is composed of a long duct and bursa, having about the same diameter as the duct.

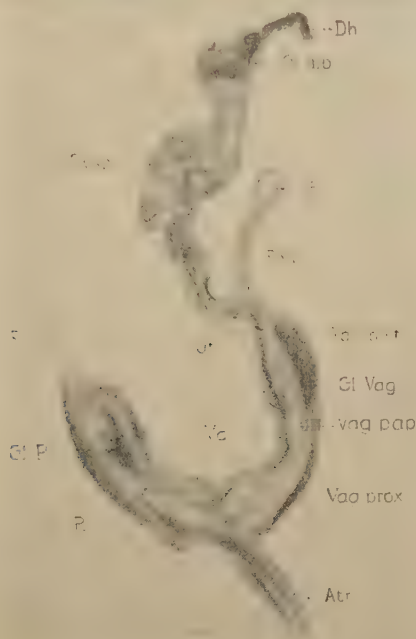


FIG. 3.—Genitalia of *Phenacolimax* (*Arabivitrina*) *riepiana* (Jickeli). Abbreviations as in fig. 1. (Mus. Basle 5813-a, prep. VI-25.)

The penis has about the same length as the vagina. The retractor muscle is inserted at the distal end of the penis and is attached to the diaphragm. The proximal end of the vas deferens enters the middle of the penis. The glandular spongy tissue in the penis is not as strongly developed as in *Phenacolimax abyssinicus* and *darnaudi*.

Mandible and radula: the median projection on the cutting margin of the mandible is rounded, and not pointed as in the other two species.

The radula shows no difference from that of *Phenacolimax abyssinicus*.

[NOTE: a specimen collected on the summit of Mt. Chillalo, about 13,000 feet, xi.1926, and placed by Connolly (1928) as "*Vitrina* sp. (?)", may possibly belong to this species. The shell was damaged but the animal, examined by Mr. Hugh Watson, was pronounced to be perfect and nearly mature. The mantle and almost the whole exposed part of the body are bluish-black. Dr. Quick, who has recently re-examined the specimen, writes (letter, 30.ix.1955) that, though much smaller, "it could very well be a young specimen of the same species" as those from Ras Degien; this must, however, remain uncertain in the absence of full-grown examples from Chillalo for comparison. At any rate melanistic Vitrinas, closely related if not identical, occur at high altitudes on Degien and Chillalo, some 365 miles apart. Dr. Foreart has kindly approved the addition of this note.—H.S.]

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SOME NEW SPECIES OF CYCLOPS SENSU LAT (CRUSTACEA : COPEPODA)

FROM NIGERIA. By SANYA D. ONABAMIRO, B.Sc., Ph.D., F.L.S.
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(With 29 text-figures.)

INTRODUCTION.

In a previous publication (Onabamiro, 1952) four new species of *Cyclops* were reported in the course of an investigation on the ecology of *Cyclops* and their relation to the incidence of *Dracunculus medinensis*, the guinea-worm, in South-west Nigeria. These four species are *Thermocyclops iroyiensis*, *Tropocyclops mellanbyi*, *Ectocyclops ilariensis* and *Halicyclops korodiensis*.

By the time the investigation was completed 30 species and subspecies of *Cyclops* were found in all, in the region under survey, of which 21 are old and nine are new. Four of these nine having been described in the paper referred to above, it is now intended to publish the description of the remaining five. These are *Mesocyclops salina*, sp. n., *Mesocyclops ogunnus*, sp. n., *Tropocyclops confinis ariensis*, subsp. n., *Tropocyclops prasinus shagamiensis*, subsp. n. and *Afrocyclops ikennus*, sp. n.

Mesocyclops salina, sp. nov. (Figs. 1-6.)

Type: Ibadan University College, index No. 5.

Female. Korodu, 24.ii.51.

Co-types in the British Museum (Natural History).

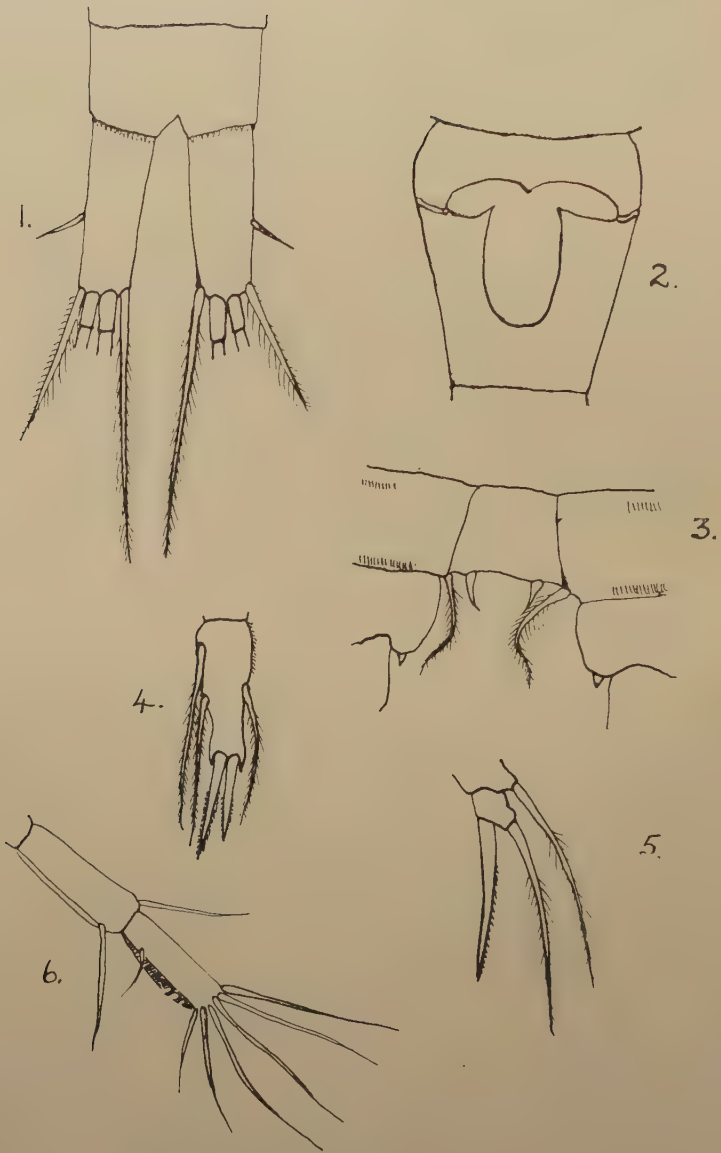
Female.—The adult specimen measures 1.0 mm. in length. The cephalothorax is roughly of the same length and width. The genital somite is 1.25 as long as it is wide and is equal to the total length of the remaining abdominal somites. The seminal receptacle is very large, and rather resembles that of *Mesocyclops longisetus* (Thiebaud) with the anterior arms slightly recurved (fig. 2).

The furcal rami are between 2.5 and 2.8 times as long as they are wide, with the lateral seta inserted at a point 58 per cent from the proximal end. There are no hairs on the inner margin of the rami.

The furcal setae are comparatively short; the middle seta (No. 3) is five-elevenths of the total length of the specimen and the innermost furcal end seta is less than twice the length of the outermost seta. The measurements of the lengths of the outer, lateral, middle, inner and dorsal furcal setae of a specimen which is 0.98 mm. long are 85, 321, 446, 142 and 64μ long and those of another specimen 1.05 mm. long are 93, 321, 446, 157, and 64μ long respectively.

The antennules are 17-jointed, and extend down to the posterior margin of the first free thoracic somite. The 16th and 17th joints both possess a hyaline membrane. That of the 16th joint is smooth, that of the 17th joint is coarsely but evenly serrated; there are three shallow notches in the hyaline membrane of this joint, not one deep notch such as is found in *Mesocyclops leuckarti* (Claus). The relative lengths of the 17 joints are shown in the table below:—

1																	17
basal	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		terminal
25	5	3	10	8	4	11	6	6	6	6	8	7	6	10	16		15



FIGS. 1-6.—*Mesocyclops salina*, sp. nov.
 1. Last abdominal segment with furcal rami.
 2. Genital somite and receptaculum.
 3. Uniting lamella of leg 4.
 4. Endopod 3 of leg 4.
 5. Leg 5.
 6. Distal joints of antennule of female.

The swimming feet are 3-jointed with the spine formula 2, 3, 3, 3. There is no seta on the basis of Leg 1. The 3rd endopod joint of Leg 4 is broad, being 2.6 times as long as it is wide, and the terminal spines are subequal; the inner spine is between 1.2 and 1.3 times as long as the outer spine and is slightly shorter than the joint (15.5 : 18). The uniting lamella of Leg 4 with its pair of pointed processes is similar to that of *Mesocyclops leuckarti* (Claus).

Leg 5 is thick-set: both the basal and second joints are short and broad. The inner spine on the second joint is shorter than the terminal seta on the joint, but the outer seta on the basal joint is very long, and extends to the same level as the inner spine.

Occurrence:—Specimens were found only in one place, in the brackish water at Korodu beach near the sea in Lagos.

The species resembles *Mesocyclops leuckarti aequatorialis* Kiefer, in having short furcal rami, pointed processes on the uniting lamella of Leg 4, three shallow notches on the hyaline membrane of the 17th antennular joint, the ratio of the lengths of the terminal spines of Leg 4, Endopod 3, and also that of the innermost and outermost furcal end setae. It is different from *M. leuckarti aequatorialis*, however, in the following respects:—

- I. The furcal rami are not quite as short as those of *aequatorialis*.
- II. The lateral arms of the seminal receptacle are shorter.
- III. The structure of Leg 5: (a) the two joints are short and broad; (b) the outer seta on the basal joint is longer than the inner spine on the second joint, whereas it is shorter in *aequatorialis*.
- IV. Habitat. This species was only found in the brackish water near the sea where the only other Cyclops found was also a new species, *Habicyclops korodiensis* (Onabamiro, 1952). It has not been found in any sample of fresh water inland and none of the species found in the latter is found in association with it.

It appears therefore that this species is quite distinct from the others in the subgenus *Mesocyclops* and I am proposing for it the name *salina* in consideration of the salty nature of its habitat.

Mesocyclops ogunnus, sp. nov. (Figs. 7–12.)

Type: Ibadan University College, index No. 6.

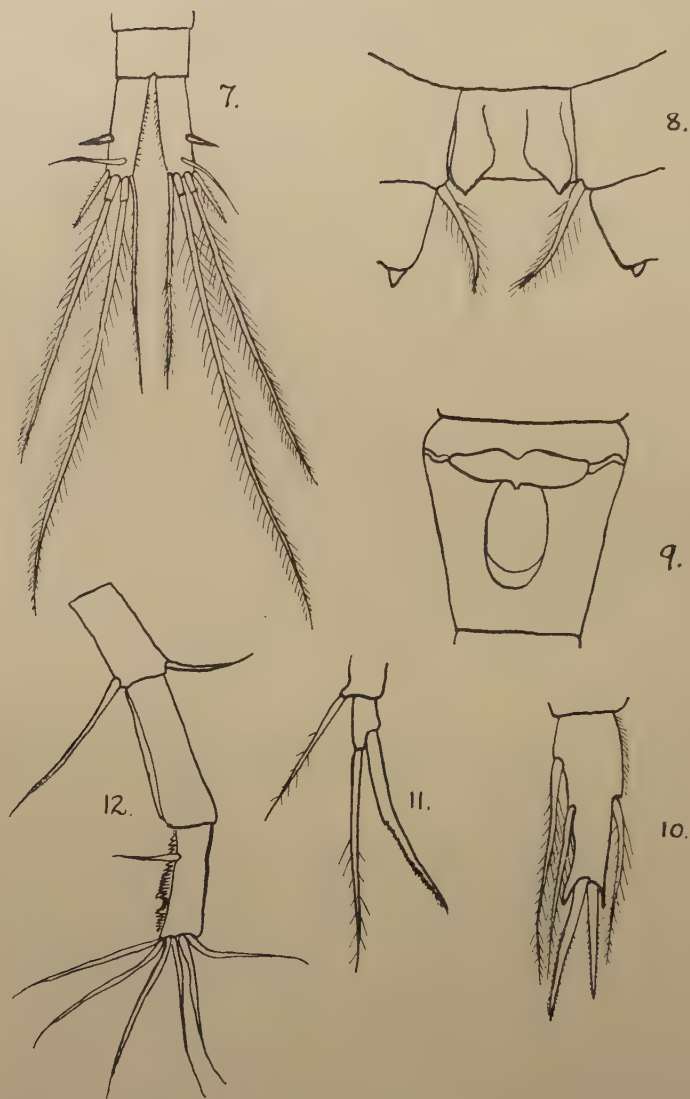
Female: Abeokuta, 3. iii. 51. Co-types in the British Museum (Natural History).

Female:—The adult specimen is between 1.0 mm. and 1.3 mm. long, minus the furcal end setae. The cephalothorax is nearly as wide as it is long. The genital somite is 1.1 times as long as it is wide. The seminal receptacle (fig. 9) slightly resembles that of *Mesocyclops thermocyclopoides* Harada.

The furcal rami are between 3.1 and 3.3 times as long as they are wide and the lateral seta is inserted at a point 60 per cent from the proximal end. The inner margins of the rami are sparsely haired.

The innermost furcal end seta is three times as long as the outermost seta, and is half the length of the middle seta (No. 3); the latter is approximately half of the total length of the specimen. In a specimen measuring 1.3 mm. the outer, lateral, middle and inner furcal setae are 100, 393, 580 and 286 μ long respectively and in another measuring 1.05 mm. long the furcal setae in the same order are 89, 357, 535, 257 and 88 μ long respectively. The dorsal setae are 100 and 88 μ long respectively.

The antennules are 17-jointed, and extend down to the middle of the first free thoracic somite. There is a smooth hyaline membrane on the 16th joint, and a coarsely serrated hyaline membrane on the 17th joint. In the latter there is one deep notch at a point about 70 per cent from the proximal end; in this respect this antennular joint resembles that of *Mesocyclops leuckarti* s. str. The 17th antennular



FIGS. 7-12.—*Mesocyclops ogunnus*, sp. nov.

7. Last abdominal segment with furcal rami.
8. Uniting lamella of leg 4.
9. Genital somite and receptaculum.
10. Endopod 3 of leg 4.
11. Leg 5.
12. Distal joints of antennule of female.

joint is much shorter than the 16th: the ratio being 15:20. The relative lengths of the 17 joints are shown in the following table:—

1 basal	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17 terminal
25	6	3	12	8	4	12	7	7	7	7	9	8	7	13	20	15

The swimming feet are 3-jointed with the spine formula 2, 3, 3, 3. There is no seta on the basis of Leg 1. The endopod of Leg 4 is longer than the exopod; the third joint is between 2.5 and 3 times as long as it is wide; of its two terminal spines the inner is sometimes found to be equal to the outer spine in length and occasionally slightly longer. The inner spine is approximately equal to the length of the joint. The uniting lamella of Leg 4 has two short conical processes on its free border.

Leg 5 is similar to that of *Mesocyclops leuckarti* s. str., except that the seta on the basal joint is short.

Occurrence:—Specimens of this species were only found in stagnant pools formed by the drying up of the River Ogun at Abeokuta; these pools were thickly covered with water-lettuce and other green plants. It would appear that this species was restricted to the dry season because as soon as the rains came and the river began to flow from late May or June it was no longer found and its place was taken by *Mesocyclops leuckarti* s. str.

This species resembles *Mesocyclops brazilianus* (Kiefer) in the structure of its furcal rami and the relative lengths of the furcal end setae but it is different from this in the shape of the seminal receptacle and that of the uniting lamella of Leg 4.

It also resembles *Mesocyclops thermocyclopoides* Harada, but the latter has the following features in which it differs from the species described here. (1) The inner margins of the furcal rami are bald. (2) Leg 4, Endopod 3 is very slim, being 3.6 times as long as it is wide. (3) The lateral setae on Leg 4, Endopod 3 extend down to the level of the posterior tip of the apical spines. (4) The outer terminal spine of this joint is not shorter than the inner terminal spine.

It seems to me, therefore, that we are here dealing with a new species quite distinct from all the other members of the subgenus *Mesocyclops*, and I am proposing for it the name *ogunnus* after the River Ogun, Abeokuta, from where the specimens were taken.

Tropocyclops confinis awiensis, subsp. nov. (Figs. 13–18.)

Type: Ibadan University College, index No. 7.

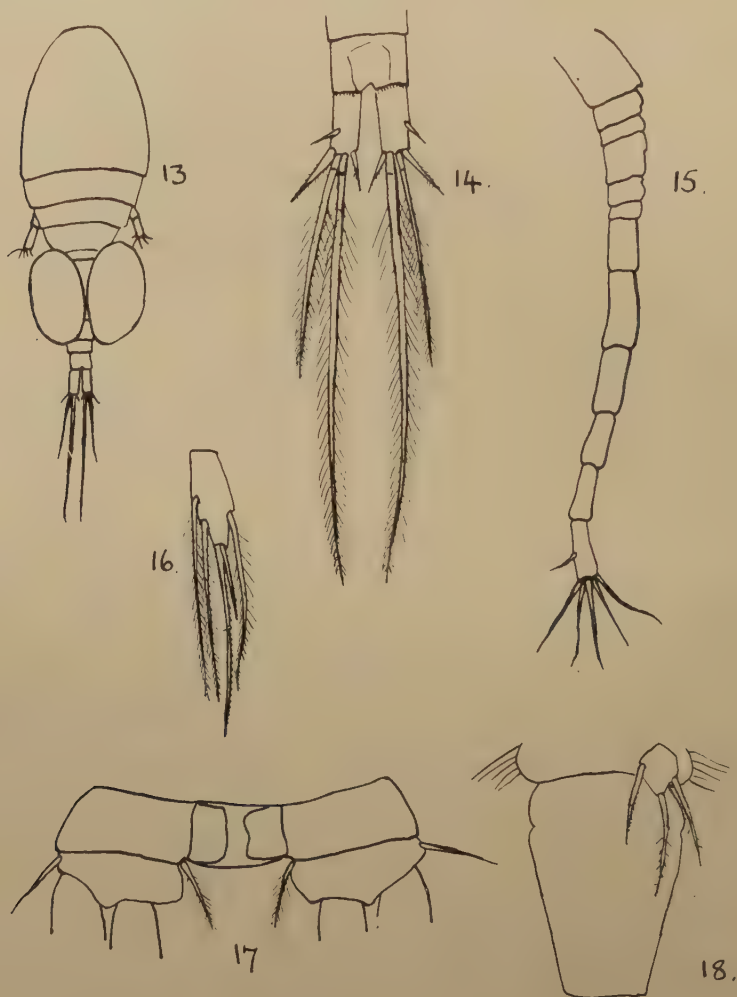
Female: River Omi, Awa, 15.iii.51. Co-types in the British Museum (Natural History).

Female:—The adult specimen is 0.5 mm. in length from the tip of the cephalothorax to the tips of the furcal rami. The anterior half of the body is oval in shape; the length of the cephalothorax is only slightly greater than its width and is 1.5 times the length of the remaining thoracic somites. The length and width of the genital somite are 64 and 57 μ long respectively while the length of the remaining abdominal somite is 89 μ .

The furcal rami are twice as long as they are wide with the lateral seta inserted at a point two-thirds from the proximal end.

The ratio of the two long furcal end setae in this subspecies is of some importance, from a systematic point of view, for it is the only *Tropocyclops* met with so far in which the lateral seta (No. 2) is only about half the length of the middle seta (No. 3).

The outermost, lateral, middle, innermost and dorsal furcal setae are 21, 114, 16 and 45μ long respectively in a specimen measuring 0.5 mm. ; on the other hand, in a slightly smaller specimen, 0.495 mm. in length, the furcal setae in the same order are 24, 114, 214, 16 and 53μ long respectively. From measurements taken



FIGS. 13-18.—*Tropocyclops confinis aviensis*, subsp. nov.

- 13. Female with egg-sacs, dorsal surface.
- 14. Last abdominal segment with furcal rami.
- 15. Antennule of female.
- 16. Endopod 3 of leg 4.
- 17. Uniting lamella of leg 4.
- 18. Leg 5.

from over a score of specimens the following ratios are found to be constant : Outermost seta to innermost seta, 1.3 to 1 ; middle seta (No. 3) to lateral seta (No. 2), 2 : 1 approximately ; dorsal seta to outermost seta (No. 1), 2 to 1 approximately.

The antennules are 12-jointed and extend down to the posterior margin of the last thoracic somite. In a position of rest they are just touching the egg-sacs. The relative lengths of the antennular joints are given in the following table :—

1 basal	2	3	4	5	6	7	8	9	10	11	12 terminal
20	11	5	13	10	4	17	25	27	20	23	25

The swimming feet are 3-jointed, with the spine formula 3, 4, 3, 3. There is no seta on the basis of Leg 1. The uniting lamellae of legs 1, 2 and 3 are convex and that of leg 4 is concave. The last joint of endopod of leg 4 is 2.3 times as long as wide : its inner terminal spine is between 2.4 and 2.6 times as long as the outer spine and between 2.1 and 2.3 times as long as the joint itself.

Leg 5 is as shown in fig. 17. It is very similar to that of *Tropocyclops confinis* Kiefer.

The egg-sacs are borne dorsally, so closely that they actually touch, covering the genital somite and the next abdominal somite.

Colour :—The body is brown with a tinge of bluish green in parts ; the antennules are pinkish.

Occurrence :—Specimens were taken from large pools of clear water in the shrinking bed of River Omi-Awa, 30 miles due south from Ibadan.

These specimens, from the description given above, bear a very close resemblance to *Tropocyclops confinis*, but the following differences are to be noted :—

(1) the relative lengths of the middle and lateral furcal end setae ; approximately 2 to 1 in these specimens, 3 to 2 in *Tropocyclops confinis*,

(2) the dorsal furcal seta is more than double the outermost furcal end seta in length in the Omi-Awa specimens, but it is less than $1\frac{1}{2}$ times as long in *Tropocyclops confinis*,

(3) the Omi-Awa specimens are distinctly smaller than any specimen of *T. confinis* found in Nigeria.

From the above observations it seems to me that the Omi-Awa specimens which so far have been found in two other places in the area under investigation are a form of *Tropocyclops confinis* which have become modified in their isolated habitat. I am therefore proposing for them the subspecific name of *awiensis*.

Tropocyclops prasinus shagamiensis, subsp. nov. (Figs. 19–24.)

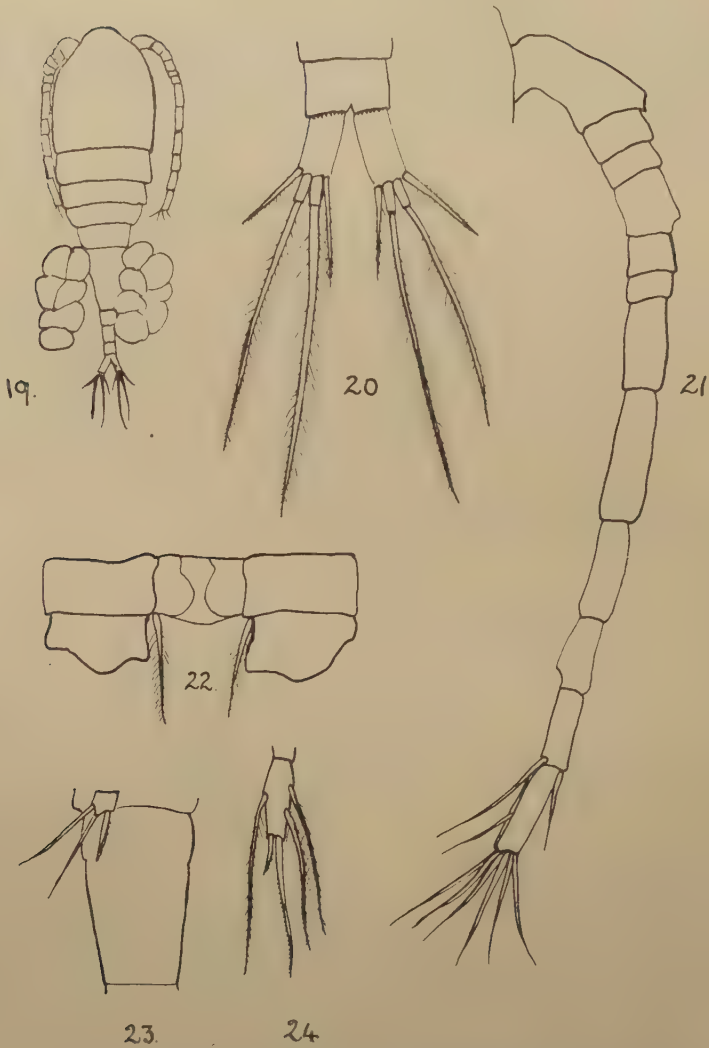
Type : Ibadan University College, index No. 8.

Female : Shagamu, 10. iv. 51. Co-types in the British Museum (Natural History).

Female :—The adult specimen is between 0.65 mm. and 0.72 mm. in length. The cephalothorax is not much longer than it is wide, the ratio of the length to the width being 1.2 : 1. The genital somite is narrow, the length being nearly double its width, and approximately equal to the lengths of the remaining abdominal somites.

The furcal rami are twice as long as they are wide, with the lateral seta inserted in the middle of each ramus. The two rami are fairly divergent.

The furcal end setae are short. The lengths of the outer, lateral, middle, inner and dorsal furcal setae of a specimen measuring 0.72 mm. are 38, 143, 171, 50 and 54μ long respectively. In specimens varying from 0.64 mm. to 0.72 mm. in length taken from places as widely separated as Ilaro in the Abeokuta Province and Ago-Iwoye and Shagamu in the Ijebu Province the ratios of the furcal setae one to another are found to be nearly the same. From these it is seen that the middle seta (No. 3) is only a little longer than the lateral seta (No. 2) and thrice the length of the innermost seta (171 : 50).



FIGS. 19-24.—*Tropocyclops prasinus shagamiensis*, subsp. nov.

- 19. Female with egg-sacs, dorsal surface.
- 20. Last abdominal segment with furcal rami.
- 21. Antennule of female.
- 22. Uniting lamella of leg 4.
- 23. Leg 5.
- 24. Endopod 3 of leg 4.

The antennules are 12-jointed and extend to the posterior margin of the third thoracic somite; the last three joints of the antennules possess a thin hyaline membrane. The relative lengths of the 12 joints are shown in the table below :—

1 basal	2	3	4	5	6	7	8	9	10	11	12 terminal
25	9	6	13	9	6	28	30	21	17	17	21

The swimming feet are 3-jointed with the spine formula 3, 4, 4, 3. There is a seta on the basis of leg 1 which extends to the second joint of endopod. The setae on the first exopod joint of legs 2, 3 and 4 are much reduced in length. The third endopod joints of legs 1, 2 and 3 have only four setae on the inner side. The last endopod joint of leg 4 is between 3 and 3.5 times as long as wide. The inner terminal spine of this joint is three times as long as the outer spine and between 1.6 and 1.8 as long as the joint itself.

The uniting lamellae of legs 1, 2, 3 and 4 are as in *T. prasinus* s. str. Leg 5 shown in fig. 71, is as in the typical form.

The egg-sacs are compact and borne on the sides of the abdomen.

Colour is light yellowish brown with a tinge of grey in the egg-sacs.

Occurrence :—Found in the stagnant side pools formed by Ibu River at Shagamu, and in similar habitats at Iaro and Ijebu.

These specimens are clearly a form of *Tropocyclops prasinus* but are different from the typical form in the following respects :—

(1) The very short middle furcal end seta which is less than four times as long as the innermost furcal seta : in *T. prasinus* s. str. the former seta is always between 5 to 6 times as long as the latter.

(2) The ratio of the inner and outer spines of leg 4, endopod 3, which is 3 : 1. In *T. prasinus* s. str. this ratio is only 2.3 : 1.

The Nigerian form is different from *Tropocyclops prasinus forma guawana* (Kiefer), *Tropocyclops prasinus jerseyensis* (Kiefer) and *Tropocyclops prasinus meridionalis* (Kiefer), both in the length of its furcal rami and in the ratio of the inner and outer spines of leg 4, endopod 3.

The nearest to this species is *Tropocyclops prasinus mexicanus* Kiefer, which it resembles in the ratio of the inner and outer spines of leg 4, endopod 3, and also in the shortness of the middle furcal end seta. It is different from this species, however, in the structure of leg 5 and in the relative lengths of the dorsal and innermost furcal setae, the former of which is shorter and the latter longer than those of *T. prasinus mexicanus*.

I regard it, however, only as a subspecies of *T. prasinus* and I am proposing for it the subspecific name of *shagamiensis* after the town of Shagamu from where specimens were first obtained.

Afrocyclus ikennus, sp. nov. (Figs. 25–29.)

Type : Ibadan University College, index No. 9.

Female. Ikenne, 24. v. 51. Co-types in the British Museum (Natural History).

Female :—The adult specimen is between 0.78 mm. and 0.9 mm. The cephalothorax is about as wide as it is long ; the fifth thoracic somite is fringed laterally with a row of long stiff hairs. The genital somite is as wide as it is long. And the seminal receptacle is as shown in fig. 26.

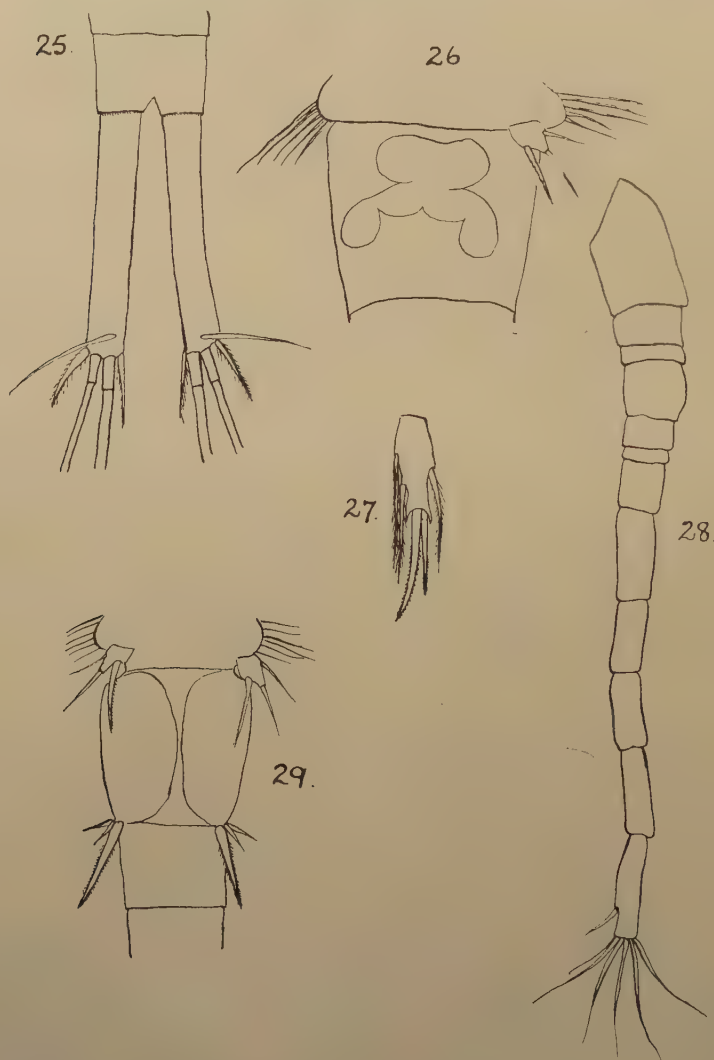
The furcal rami are on the average seven times as long as they are wide with the lateral seta inserted at a point 82 per cent from the proximal end ; both the outer and the inner edges are smooth. The rami are very divergent at base.

The innermost and outermost furcal end setae are of equal length in the majority of specimens found ; the innermost seta is one-third of the length of the furcal ramus, and the middle seta (No. 3) is two-fifths of the total length of the specimen. The outer, lateral, middle and inner furcal end setae of a specimen which is 0.945 mm. long are 35, 214, 364 and 35 μ long and those of another specimen 0.78 mm. long are 36, 207, 357 and 32 μ long respectively. The dorsal seta varies between 50 and 56 μ long.

The antennules are 12-jointed and extend only down to the level of the cephalothorax. The lateral seta on the 12th antennular joint is inserted at a point 75 per

cent from the proximal end. The relative lengths of the 12 joints are shown in the table below :—

1 basal	2	3	4	5	6	7	8	9	10	11	12 terminal
15	4	3	7	5	2	6	12	9	10	12	14



FIGS. 25-29.—*Afrocylops ikkennus*, sp. nov.
 25. Last abdominal segment with furcal rami.
 26. Genital somite of female showing receptaculum and leg 5.
 27. Endopod 3 of leg 4.
 28. Antennule of female.
 29. First and second abdominal segments of male.

The swimming feet are 3-jointed with the spine formula 2, 3, 3, 3. There is a seta on the basis of leg 1; this seta extends to the level of the posterior margin of the third endopod joint. The third endopod joint of leg 4 is between 2 and 2.3 times as long as it is wide; its inner terminal spine, curved inwards, varies between 1.33 and 1.5 times as long as the outer spine and between 1.25 and 1.39 times as long as the joint itself. Leg 5 is a flat triangular plate as long as it is wide. It bears an inner spine and an outer seta both inserted at points in the middle of the plate, and an apical seta. The inner spine is slightly longer than the apical seta, which is 1.5 times as long as the outer seta.

The egg-sacs are long; they extend down to the posterior margin of the furcal rami.

Colour.—The colour of the body is brown and that of the egg-sacs is light green.

Remarks.—F. Kiefer, 1939, reviews the subgenus *Afrocylops* as a whole and described species found in East and South Africa. Kiefer's list comprises *Afrocylops gibsoni* (Brady), *A. doryphorus* (Kiefer), *A. lanceolatus* (Kiefer), *A. curticornis* (Kiefer), *A. alter* (Kiefer), *A. propinquus* (Kiefer) and *A. nubicus* (Chappius).

Of these the Nigerian species is nearest only to *Afrocylops gibsoni* (Brady) with which it was found in common in the same brooks. It was first thought to be another variety of *Afr. gibsoni*, but the following differences were found:—

1. The inner spine of Leg 5 is slightly longer than the apical seta in this new species, whereas it is smaller than the apical seta in *Afr. gibsoni*.
2. The inner terminal spine of Leg 4, End. 3 is 1.4 times as long as the joint in this new species whereas, it is equal in length to the joint in *Afr. gibsoni*.
3. The relatively greater length of the middle seta (No. 3) in this new species.
4. The shape of the seminal receptacle.
5. The colour, which is brown, while specimens of *Afr. gibsoni* found in close association with it in the same brooks and found alone elsewhere were all yellowish green in colour.

It seems from the above considerations that we are dealing with a new species for which I am proposing the name *ikennus*, after the town Ikenne, Ijebu-Remo, where the specimens were first obtained.

ACKNOWLEDGMENTS.

The writer is indebted to the Colonial Medical Research Committee for a grant to the Parasitology Research Laboratory, University College, Ibadan, which enabled the work to be carried out, to Professor R. M. Gordon of the Liverpool School of Tropical Medicine for the use of some instruments, to Dr J. P. Harding of the Crustacea Department, Natural History Museum, London for some valuable suggestions and to the junior members of the research team for their loyal cooperation.

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STUDIES IN DIURNAL RHYTHMS.—V. NOCTURNAL ECOLOGY AND WATER-RELATIONS OF THE BRITISH CRIBELLATE SPIDERS OF THE GENUS *CINIFLO* BL. By J. L. CLOUDSLEY-THOMPSON, M.A., Ph.D., F.R.E.S., F.L.S., F.Z.S. (Department of Zoology, University of London King's College).

(With 7 text-figures.)

[Read 21 April 1955.]

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I. INTRODUCTION.

For some years the writer has been engaged in studying the physiological basis of diurnal rhythms in the Arthropoda (Cloudsley-Thompson, 1951 a, 1952 a, c, 1953 a, b, c, etc.) and in trying to evaluate its ecological significance (1954 a, b). As a result of this work it has been suggested that terrestrial arthropods can be divided ecologically into two main groups. The first of these includes woodlice, centipedes, millipedes and their allies: these lose water rapidly in dry air and consequently are nocturnal and restricted to damp, dark habitats (Cloudsley-Thompson, 1950 b, 1951 b; Edney, 1951). The second group contains most insects, spiders and other arachnids which are comparatively independent of moist surroundings because their integument possesses an impervious layer of lipid that prevents desiccation (Davies & Edney, 1952; Lees, 1947; Wigglesworth, 1945, etc.). A number of the latter, however, have become secondarily adapted to the nocturnal habit. These include a few highly specialized forms whose food is more readily available at night or occurs in dark places and the inhabitants of deserts and other regions with a rigorous hot climate. Finally it has been suggested (Cloudsley-Thompson, 1954 a) that primitive orders and the more primitive species of higher orders may have become nocturnal as a result of competition with more efficient types. The present study was designed to cast light on the above hypotheses.

Two British species of the genus *Ciniflo* were selected for investigation and a number of experiments were also carried out on the third species of the genus found in this country. Although the results obtained neither helped to prove, or to disprove the original hypotheses, they clearly indicate the close relationship between the physiology and ecology of these three species, several interesting aspects of which have emerged.

II. MATERIAL AND NOMENCLATURE.

Three species of cribellate spiders belonging to the genus *Ciniflo* Blackwall are found in the British Isles. They are: *C. ferox* (Walckenaer, 1825), *C. similis* Blackwall, 1845 and *C. fenestralis* Stroem, 1768. All these species occur in my own and neighbouring gardens at Esher, Surrey.

These spiders are somewhat alike in general appearance, especially *C. similis* and *C. fenestralis*, although the former usually reaches a greater size. *C. ferox*, the largest of the three, has a dark, sinister appearance, is decidedly fierce and, like *C. similis*, will sometimes plunge its jaws into the finger of its captor, although the effect of the bite is very slight. It is unlikely to be confused with its congeners. Nearly 98 per cent of *C. ferox* found in Esher were of the dark, melanic variety.

The generic name *Amaurobius* C. L. Koch, 1837 was generally used in place of *Ciniflo* Bl., both in this country and abroad (Petrunkevitch, 1928, 1939), until Bristowe (1939) pointed out that *Coelotes* Blackwall, 1841 is a synonym of *Cavator* Blackwall, 1840 and *Cavator* a synonym of *Amaurobius* C. L. Koch, 1836. In the latter publication Koch only included the species *roschidus* and *tigrinus* in the genus *Amaurobius*: the identity of *roschidus* is uncertain, so *tigrinus*, which is a synonym of *atropus* Walck. (fam. Agelenidae) became the type species for the genus *Amaurobius*. Consequently species previously included in the European genus *Coelotes* were transferred to *Amaurobius* and species previously in *Amaurobius* to *Ciniflo* Blackwall, 1840, a generic name that had already been reintroduced by F. O. Pickard-Cambridge. Locket & Millidge (1951) in Britain have followed Bristowe in this matter, but abroad *Amaurobius* is still generally used (e.g. by Chamberlin, 1947; Kaston, 1948; Gertsch, 1949; Millot, 1949). This discrepancy apparently arises partly from the fact that Koch used the name *Amaurobius* for spiders of different genera in two almost contemporary publications: *Uebersicht des Arachnidensystems*, Nürnberg, Heft 1, 1–39 (1837) and 'Arachniden' in Panzer, G. W. F., *Faunae Insectorum Germaniae initia Deutschlands Insekten*, Regensburg, Heft 141, fol. 3–6, which was published on 1 October 1836. An additional complication is introduced by the fact that in consequence of a misprint 'Heft 151' appears instead of 'Heft 141' in Bristowe (1939). According to Bonnet (1945), Heft 141 was published in 1837, but details of Heft 151 are naturally not given as it does not include any spiders. However, Schenkling (1939) pointed out that Heft 151 did not appear until 1837, the same year that *Uebersicht des Arachnidensystems* was published, and for this reason Kaston (1948), believing this to be the relevant Heft, retained *Amaurobius* for the cribellate genus; but Schenkling agreed that Heft 141 was published in 1836. The validity of *Ciniflo* Bl. is therefore established.

This matter has been discussed at some length in the hope that by so doing the controversy may be finally settled*.

III. DISTRIBUTION.

All three species are widely distributed in Europe and the British Isles though *C. ferox* becomes scarce in Scotland and only *C. fenestralis* has been recorded from the Orkneys and Shetlands (Bristowe, 1931).

They are to be found under logs and stones, in holes in walls and under bark where they spin their bluish meshed webs. Although there is no precise restriction of territory, *C. fenestralis* is commonly associated with the bark of trees, *C. similis* with walls, fences and outhouses and *C. ferox* with similar but usually damper situations. The territories overlap. In the warm, humid conditions found in the Scilly Islands and the coastal fringes of Cornwall *C. ferox* extends its usual range to open heathland, etc. (Bristowe, 1929, 1935; Cloudsley-Thompson, 1956 a).

* Since this was written, P. Bonnet (1955, *Bibliographia araneorum*. Toulouse, 2 (1) 272) has recognised *Amaurobius* for the cribellate genus.

C. similis is one of our commonest house-spiders and males, in particular, roam about the walls at night in autumn, winter and spring months. In damper houses it may be joined by *C. ferox*, and both are often to be found in cellars.

Thus *C. ferox* and *C. fenestralis* tend to occur in damper places than does *C. similis*. This was well illustrated by an investigation of a pile of logs on damp ground made on 25 October 1953, in which seven adult and many immature *C. ferox* were found but no *C. similis*, although four adult specimens of the latter species were taken from the interstices between a number of upright posts nearby where only two *C. ferox* were found. *Steatoda bipunctata* (L.), a species usually found in dry places, was very common in the second locality. Again on 29 November 1953 I found five adult *C. similis* between the top ten of a stack of twenty-four old tiles. There were no *C. ferox* among these, but between the lower fourteen tiles from which *C. similis* were absent I found no less than nine adult and several immature specimens of *C. ferox*. The relative humidity of the air in the spaces between the tiles was measured by means of an Edney paper hygrometer. In the upper layers 94 per cent relative humidity was recorded, in the lower layers a reading of 99 per cent was obtained. These values can only be regarded as approximate, since paper hygrometers, even after calibration, are inaccurate at the extremes of their range. Nevertheless there can be little doubt that the humidity was greater between the lower tiles of the stack.

IV. THE DIURNAL RHYTHM OF LOCOMOTORY ACTIVITY.

In recent years the phenomenon of 24-hour periodicity in animals has attracted considerable attention and it is evident that diurnal rhythms are common and manifest in diverse ways. From a physiological point of view they can be divided into two basic types: 'exogenous', a direct response to environmental changes and 'endogenous' rhythms which persist under constant conditions. Most species of animals show a combination of both types and such rhythms are termed 'composite'. Endogenous rhythms are frequently correlated with changes in environmental factors such as light, temperature and humidity. As they are not a direct response to these, however, such factors are referred to as 'clues' by the writer (Cloudsley-Thompson, 1952 a, c, 1953 b), a term which appears to correspond to the German 'Zeitgeber' (Aschoff, 1954), and their importance lies in the maintenance of the rhythm and in keeping it in phase with the environment.

Under natural conditions there are probably several clues active at the same time, of which one is generally the ruling factor of an animal's periodicity. However, there can be competition between different clues and changes in the sensitivity and physiological state of an animal may engender considerable changes in the relationship of the various environmental factors involved (Cloudsley-Thompson, 1952 a).

In contrast to insects and crustaceans little work has yet been carried out on diurnal rhythms in the arachnids and in the case of spiders practically nothing is known of the physiological basis of such rhythms, although their ecological significance has been discussed by a few authors. Thus Park & Strohecker (1936) found that in climax forest a number of nocturnal spiders including *Ciniflo* (*Amaurobius*) *bennetti* Bl. began their nightly hunt for prey promptly at dusk and they correlated the onset of this activity with decreasing light intensity. Later Park (1938) found, both by field observation and by means of recording apparatus, that the Panama tarantula *Sericopelma rubronitens* Auss. was nocturnal under natural conditions, 97 per cent of its locomotory activity taking place during the hours of darkness. According to Lowrie (1942), the spiders of the xeric dunelands in the Chicago area show the characteristics of animals living in dry, open lands, and cursorial burrowing and nocturnal habits are well represented.

More recently Muma & Muma (1949) analysed sweep-net catches made at various times of the day and night, and in this way found that the nocturnal hunting-spider *Oxyopes salticus* Hentz. reached a distinct peak of activity in the late evening

in high prairie and tall climax grass and a light peak in the afternoon and evening in deciduous shrubs, possibly as a result of early shading in the latter locality. Finally a study of the ecology of spiders of maritime drift-lines (Barnes & Barnes, 1954) showed that the greatest amount of migration out of the drift occurred at night.

(a) *Effect of light, temperature and humidity.*

In the present study the daily rhythm of locomotory activity in the three species of *Ciniflo* was measured by means of aktograph apparatus. This consisted essentially of a box pivoted about its median transverse axis so that any movement of the spider within caused it to tip. The boxes were connected by threads to gymbal levers writing on barograph drums acting as miniature kymographs. The whole apparatus could be placed in a large incubator where light and temperature were artificially controlled (Cloudsley-Thompson, 1952 b, 1953 c). During each experiment the temperature and relative humidity of the air were measured with a recording thermo-hygrograph. An 18-hour and a 24-hour time-switch were used to provide light and temperature cycles of different frequency. When the apparatus was in the incubator, lighting consisted of a 15-watt pearl bulb at approximately 10 cm. distance from the arena of the aktographs. The smoke drum records obtained were analysed at the end of each week; the number of times that the spider crossed an axis and caused the arena to rock in each 3-hour period was counted and plotted as block histograms.

Some of the results obtained are given in figs. 1 and 2. Fig. 1 shows the daily rhythm of activity in all three species in natural daylight and darkness at room temperature and humidity. It can be seen from this that the greatest amount of

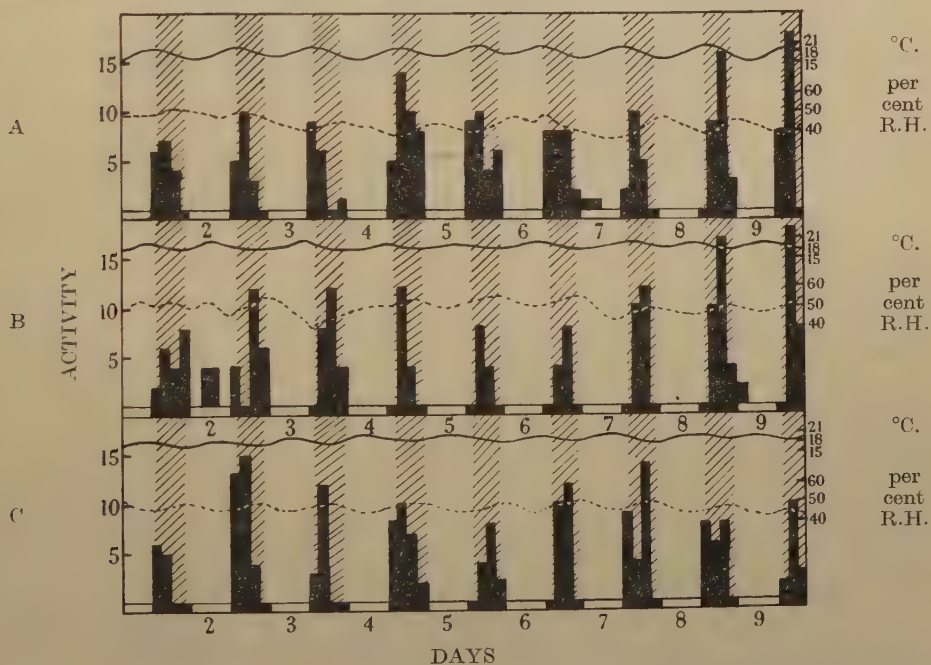


FIG. 1.—Analysis of aktograph records showing diurnal rhythm of movement and rest in spiders of the genus *Ciniflo* in natural daylight and darkness at room temperature and humidity. Ordinates: activity on the left, temperature and relative humidity on the right. Abscissa: time in days. The black strips represent 12-hour periods from 18.00 to 06.00 hours. A. Periodicity in *C. ferox*. B. Periodicity in *C. similis*. C. Periodicity in *C. fenestralis*. Further explanation in the text.

activity takes place in the early part of the night, which is typical of most nocturnal species. In fig. 2 are given some aktograph records showing the rhythm of movement and rest in *C. ferox* under controlled conditions of lighting and temperature. When six hours of light alternated with 18 hours of darkness (a 24-hour cycle) a

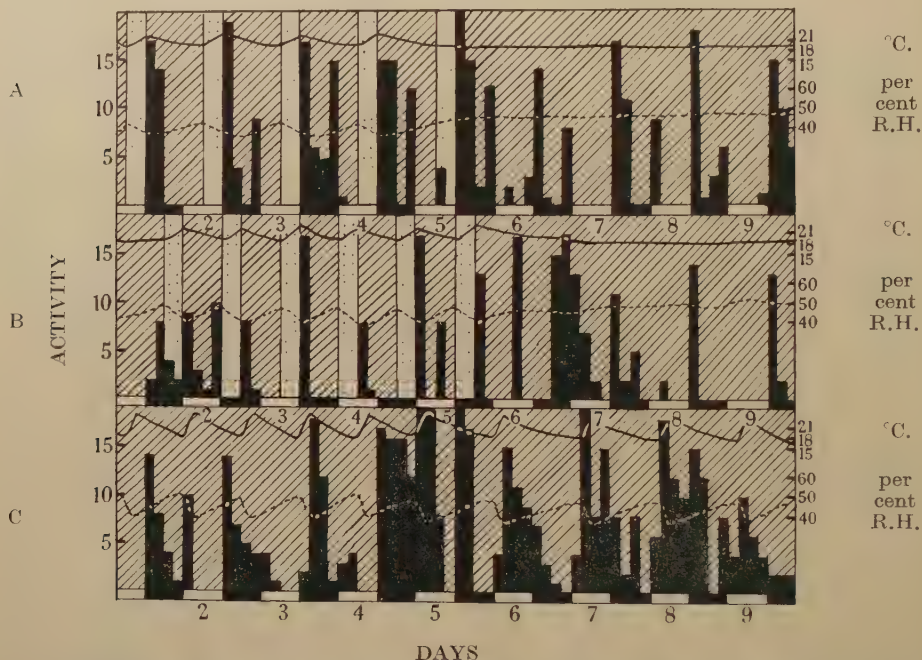


FIG. 2.—Analysis of aktograph records showing the effect of alternating artificial light and fluctuating temperature on the diurnal rhythm of movement and rest in *C. ferox*. Conventions as in fig. 1. A. Effect of six hours of light alternating with 18 hours of darkness (a 24-hour cycle) followed by constant darkness. B. Effect of six hours of light alternating with 12 hours of darkness (an 18-hour cycle) followed by constant darkness. C. Effect of 18 and 24-hour temperature cycles. Further explanation in text.

rhythm was set up which persisted in constant darkness at constant temperature and relative humidity (fig. 2A). However, when six hours of light alternated with 12 hours of darkness (an 18-hour cycle) a less marked rhythm was set up which did not persist in constant darkness but was replaced by a 24-hour rhythm (fig. 2B). Finally an 18-hour cycle of temperature fluctuation in constant darkness did not set up a rhythm, but a 24-hour cycle of temperature fluctuation engendered a rhythm of activity with its peak at the highest temperature (fig. 2C). From these and a number of other records it is concluded that the diurnal rhythm of movement and rest in *C. ferox* is a composite one, controlled primarily by alternating light and darkness, but in the absence of this a rhythm can be set up by a 24-hour cycle of temperature fluctuations, but not by an 18-hour cycle. At the same time 18-hour cycles of alternating light and darkness set up a weaker locomotory rhythm than that caused by a 24-hour cycle, as occurs in the cockroach, *Periplaneta americana* (L.) according to Cloudsley-Thompson (1953 b) and this is replaced by the normal 24-hour rhythm under constant conditions, indicating the persistence of the endogenous factor of the rhythm.

(b) Intensity of nocturnalism.

The experiments on the water-relation of the integument to be described below suggest that *C. ferox* loses water through its lung-books more rapidly than does

C. similis, although the critical temperature of the cuticular lipid layer of each is about 35° C. It seemed possible that this might be correlated not only with a preference for moister habitats, but also in more markedly nocturnal habits. In order to test this hypothesis, ten spiders (2 males, 8 females) of each species were placed singly in the aktograph for periods of seven days, during which they were illuminated for 12 hours from 18.00 to 06.00 hours daily, and were in darkness from 06.00 to 18.00 hours G.M.T. During the light periods the temperature rose to 25° C. while the relative humidity fell to 35 per cent: during the periods of darkness the temperature dropped to 20° C. and the relative humidity rose to 43 per cent. The gross activity of each spider during one week was thus determined and the percentage of this that took place during the periods of darkness calculated. It was found that the average number of times that *C. ferox* caused the aktograph to rock during a week was 257, whilst for *C. similis* the number was 261. The percentage of nocturnal activity, that is activity taking place during the periods of darkness, was 91 per cent in *C. ferox*, whilst in *C. similis* it was 93 per cent. The differences between these figures for the two species are, however, not statistically significant, nor was there any marked difference between the activity of the two sexes.

Perhaps it was naive to hope that a slight effect on which natural selection might have been operating over a considerable period of time could be demonstrated by a comparatively crude experiment. Nevertheless it must be assumed that the intensity of nocturnalism is the same in the two species, even though in preliminary experiments there was some slight indication that it was greater in *C. ferox* than in *C. similis* (Cloudsley-Thompson, 1954 a).*

V. WATER-RELATIONS OF THE INTEGUMENT.

The success on land of the arachnids, like that of the insects, depends upon the presence of an epicuticular layer of lipid which prevents the loss of water by evaporation and renders the animals comparatively independent of moist conditions (see discussion in Cloudsley-Thompson, 1954 a). It is well known that in insects there is a critical temperature characteristic for each species, at which the cuticular wax-layer undergoes a physical change. Above this temperature the rate of water-loss by evaporation through the cuticle is very much increased (Wigglesworth, 1948). Lees (1947) has obtained similar results with various species of ticks, and the writer with four species of scorpions (Cloudsley-Thompson, 1956 b).

Comparatively little information concerning the effect of temperature on the evaporation of water from spiders has yet been obtained, but Palmgren (1939) found that evaporation rose steadily with temperature in *Dolomedes fimbriatus* (Clerck), although he did not work at temperatures sufficiently high to demonstrate the presence of a 'critical point'. More recently Davies & Edney (1952) have shown that the rate of evaporation increased rapidly above 40° C. in the spiders *Lycosa amentata* (Clerck), *Tegenaria domestica* (L.) (= *T. derhami* Scop.), *Meta segmentata* Clerck, *Zygiella atrica* (C. L. Koch) and *Z. x-notata* Clerck. These results indicate that spiders resemble insects and ticks and differ from woodlice and myriapods as far as the effect of temperature upon evaporation is concerned, and suggest that a discrete layer of wax is probably present in the spider cuticle.

(a) Temperature and water-loss.

The rate of water-loss per hour in *Ciniflo* spp. was ascertained by suspending weighed spiders over anhydrous phosphorus pentoxide in conical flasks immersed in a water bath maintained at the required temperature for periods of 15 or 20 minutes. The rate of water-loss was expressed as mg./cm.²/hr., the surface area of each spider being established by substitution in the formula $S = kW^{\frac{2}{3}}$.

A value of $k=12$, determined by flattening over squared paper the integument of a number of spiders of known weight, was used. This compared with $k=12.3$

* Recently I have been able to show that in woodlice the degree of nocturnal activity is correlated with the ability to withstand water-loss by transpiration (Cloudsley-Thompson, 1956 c.)

in *L. amentata* according to Davies & Edney (1952). The value of k need only be approximate however because specific differences in evaporation are often so great that an error of 50 per cent will not affect the conclusions drawn (Wigglesworth, 1945).

A large number of measurements were carried out using all three species of *Ciniflo*. In some cases the lung-books and spiracles were blocked with celloidin; in others intact spiders were used. The results are presented in figs. 3 to 6. In fig. 3 the rate of evaporation from 15 adult female *C. ferox* with lung-books and

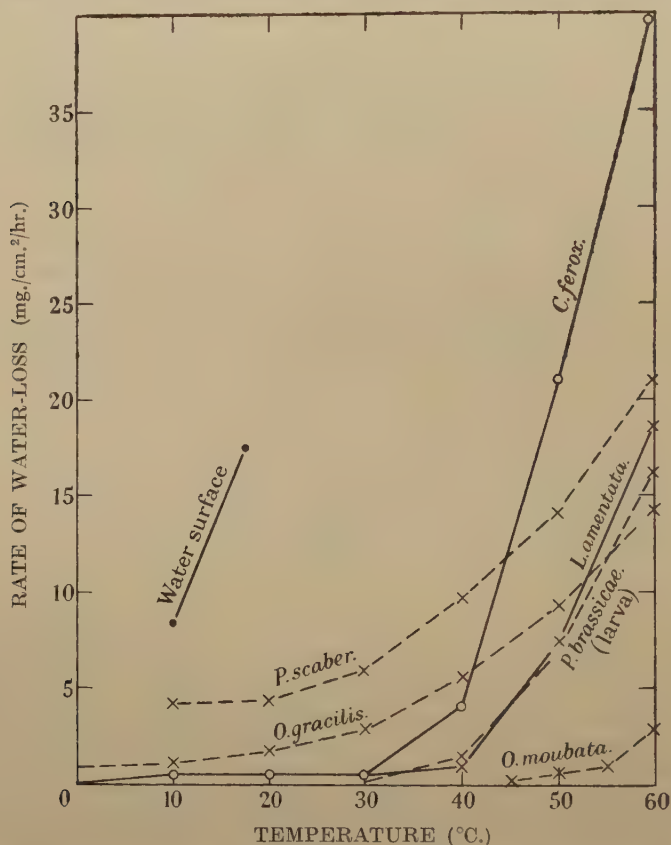


FIG. 3.—Rate of water-loss from adult female *C. ferox* with lung-books and spiracles blocked, exposed for 15 minutes to dry air at various temperatures; compared with a water surface, *Pieris brassicae* larvae, *Porcellio scaber*, *Oxidus gracilis*, *Lycosa amentata* and *Ornithodoros moubata*.

spiracles blocked, exposed for periods of 15 minutes to dry air at various temperatures, is compared with that of an open water surface, *Pieris brassicae* L. larvae (data from Wigglesworth, 1945), the woodlouse *Porcello scaber* Latr. (data from Edney, 1951), the millipede *Oxidus gracilis* (C. L. Koch) (data from Cloudsley-Thompson, 1950 b), the tick *Ornithodoros moubata* (Murray) (data from Lees, 1947) and the spider *Lycosa amentata* (Clerck) (data from Davies & Edney, 1952). This illustrates clearly the absence of a critical point in the woodlouse and millipede, and indicates that that of *C. ferox* is lower than those of the other arachnids and the insect.

In fig. 4 the rate of water-loss at different temperatures in dry air of five specimens of each of the species with lung-books and spiracles blocked is given, while fig. 5 indicates the rates of water-loss in five intact specimens of each species. It can be seen that the scatter of results is greater with the intact spiders. Fig. 6 shows the

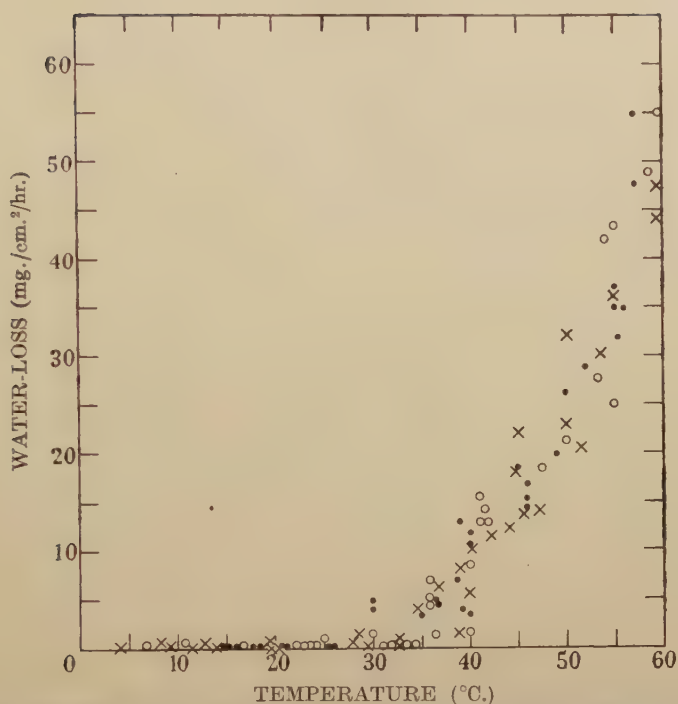


FIG. 4.—Rate of water-loss in dry air at different temperatures from *C. ferox* . . . x; *C. similis* . . . o; *C. fenestralis* . . . •. Lung-books and spiracles blocked.

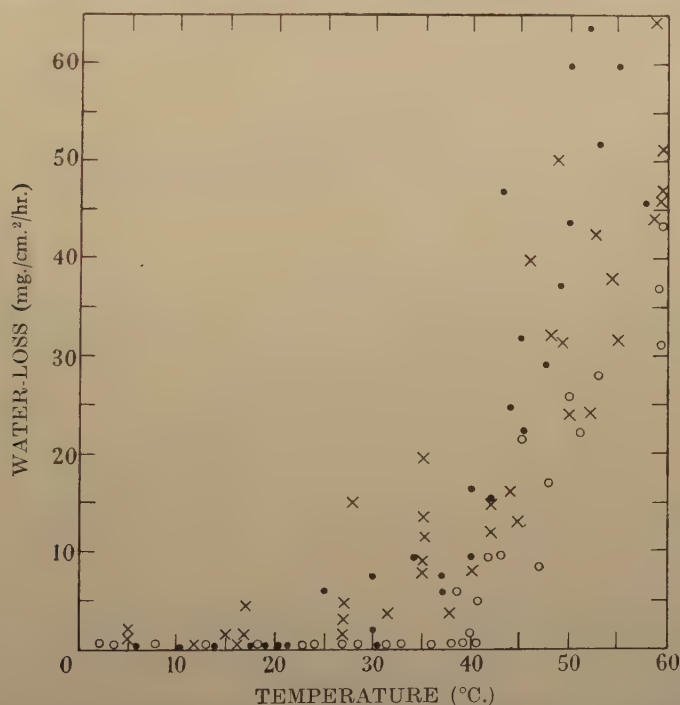


FIG. 5.—Rate of water-loss in dry air at different temperatures from *C. ferox* . . . x; *C. similis* . . . o; *C. fenestralis* . . . •. Intact spiders.

results of similar experiments with intact spiders carried out in an atmosphere containing approximately 10 per cent of carbon dioxide to keep the lung-books and spiracles open. The spiders were alive at the outset of each experiment but died as higher temperatures were reached.

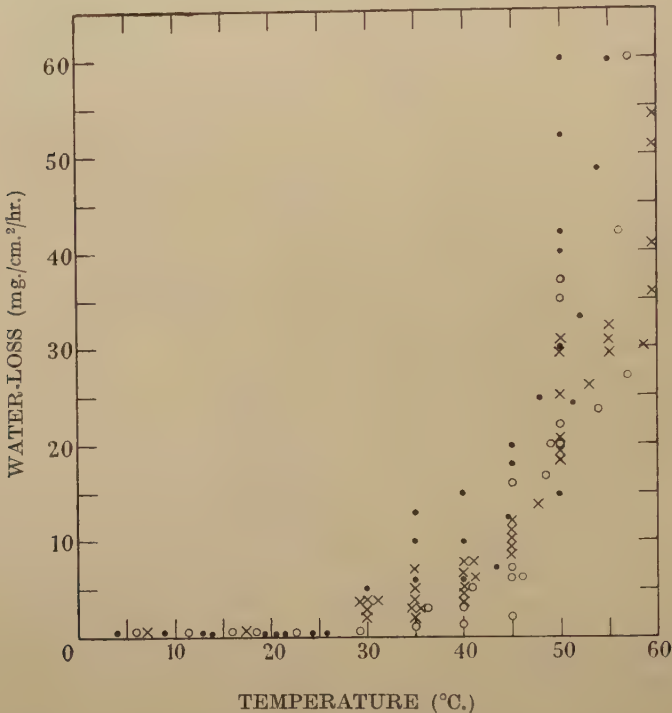


FIG. 6.R.—Rate of water-loss in dry air at different temperatures from *C. ferox* . . . x; *C. similis* . . . o; *C. fenestralis* . . . •. Intact spiders in an atmosphere containing 20 per cent carbon dioxide.

From the above it is concluded that there is a critical point at approximately 35° C. in all three species, but in the intact spiders the rate of water-loss below this critical point is appreciably greater in *C. ferox* and *C. fenestralis* than in *C. similis*, indicating a greater rate of evaporation through the lungs in these two species.

(b) The effect of carbon dioxide.

In order to determine more accurately the effect of carbon dioxide on the rate of water-loss by evaporation, five spiders of each of the three species of *Ciniflo* were placed in desiccators in which the relative humidity was maintained at 50 per cent by means of diluted sulphuric acid and their rate of water-loss during 48 hours at room temperature ($20^{\circ} \pm 1^{\circ} \text{C.}$) noted. In order that the spiders could be weighed before and after the experiment, they were anaesthetized with ether and harnessed by a thread of cotton tied around the prosoma between the coxae of the third and fourth pair of legs. Great care had to be taken in harnessing the spiders because if their legs became entangled in the thread, on regaining consciousness they damaged themselves in their struggles and subsequently lost weight very rapidly.

The results of these experiments are given in Table I and indicate that the rate of water-loss is greater in *C. ferox* than in *C. similis*, and greater still in *C. fenestralis*.

TABLE I.—Rate of water-loss in mg. cm.²/hr. of living spiders during 48 hours at room temperature $20^{\circ} \pm 1^{\circ} \text{C.}$ at a relative humidity of 50 per cent.

<i>C. ferox</i>		<i>C. similis</i>		<i>C. fenestralis</i>	
Weight in mg.	Rate of water-loss	Weight in mg.	Rate of water-loss	Weight in mg.	Rate of water-loss
246	0.25	73	0.09	48	0.38
169	0.17	136	0.18	42	0.43
101	0.27	85	0.19	42	0.26
110	0.23	135	0.12	59	0.23
127	0.14	129	0.17	32	0.53
Means 151	0.21	111	0.15	45	0.37

The sulphuric acid mixtures were now replaced by calcium chloride and the experiments repeated over 24 hours, using 10 specimens of each species, both in normal air and air containing about 10 per cent of carbon dioxide. The results of the second series of experiments are given in Table II, from which it can be seen that the rate of water-loss was nearly doubled by the presence of carbon dioxide which kept the lung-books open. At the same time it is again evident that the rate of water-loss through the lung-books varies considerably in the three species.

TABLE II.—Rate of water-loss in mg./cm.²/hr. of living spiders during 24 hours at room temperature $20^{\circ} \pm 1^{\circ} \text{C.}$ in dry air and in air containing a high proportion of carbon dioxide.

<i>C. ferox</i>				<i>C. similis</i>				<i>C. fenestralis</i>			
AIR		AIR + CO ₂		AIR		AIR + CO ₂		AIR		AIR + CO ₂	
Init. wt. in mg.	Rate of water-loss	Init. wt. in mg.	Rate of water-loss	Init. wt. in mg.	Rate of water-loss	Init. wt. in mg.	Rate of water-loss	Init. wt. in mg.	Rate of water-loss	Init. wt. in mg.	Rate of water-loss
176	0.24	182	0.54	125	0.12	121	0.20	54	0.40	50	0.83
154	0.26	179	0.55	120	0.17	116	0.44	53	0.31	50	0.42
153	0.21	154	0.43	118	0.09	115	0.16	50	0.42	36	0.83
131	0.20	147	0.54	101	0.05	96	0.21	34	0.23	33	0.66
111	0.20	116	0.39	97	0.06	96	0.08	31	0.23	32	0.66
103	0.49	93	0.69	85	0.25	81	0.58	30	0.63	31	0.83
97	0.49	87	0.44	73	0.24	80	0.25	26	0.17	29	0.83
64	0.45	58	0.49	66	0.14	69	0.24	25	0.34	27	0.42
59	0.37	55	0.57	50	0.16	47	0.16	25	0.31	27	0.73
53	0.21	52	0.57	38	0.62	38	0.73	15	0.55	21	0.97
Means 110	0.31	112	0.52	87	0.19	86	0.31	34	0.36	34	0.67

(c) *Water-loss and survival.*

The times of survival of five specimens of each species in the desiccators in which the relative humidities were controlled at 50 per cent and 0 per cent as before, at room temperature ($19^{\circ} \pm 1^{\circ} \text{C.}$), are given in Table III. It can be seen that survival is longer in *C. similis* than in *C. ferox* and shortest in *C. fenestralis*. Death ensues when from 20 to 25 per cent of the total weight has been lost by evaporation.

However, these figures probably bear little relation to survival under natural conditions because the spiders were denied the shelter of their retreats which normally protect them from the desiccating effect of the atmosphere. In addition, the harnessing thread hampered their movements and prevented them from spinning any form of shelter. It was noticed too that a few spiders which escaped from their harness tended to live longer than the others to which a cotton thread remained attached. The figures for such spiders that escaped however are not included in Table III, the significance of which lies in the comparative times of survival of the three species under equally abnormal conditions.

(d) *Respiratory organs and water-loss.*

The experiments described above suggest that the efficiency of the cuticular lipid layer is similar in the three species of *Ciniflo*, but that more water is lost by evaporation through the lung-books in *C. ferox* than in *C. similis*, and more still in

TABLE III.—Number of days survival, per cent water-loss at death and rate of water-loss during desiccation at room temperature ($19^{\circ} \pm 1^{\circ} \text{C.}$) in *Ciniflo ferox*, *C. similis* and *C. fenestralis*.

<i>C. ferox</i>				<i>C. similis</i>				<i>C. fenestralis</i>			
Init. wt. in mg.	Survival in days	Per cent loss in wt.	Rate of water-loss mg./cm. ² /hr.	Init. wt. in mg.	Survival in days	Per cent loss in wt.	Rate of water-loss mg./cm. ² /hr.	Init. wt. in mg.	Survival in days	Per cent loss in wt.	Rate of water-loss mg./cm. ² /hr.
Percent R.H. {	248	6	28	136	10	29	·18	26	4	26	·42
	172	10	15	118	7	26	·14	24	4	25	·31
	81	4	16	73	7	27	·09	22	4	29	·42
	72	7	36	49	9	17	·10	17	3	23	·53
	34	5	32	45	8	30	·16	16	5	12	·13
Mean 121	6	25	·22	84	8	26	·14	21	4	23	·36
Percent R.H. {	124	5	29	97	7	15	·11	30	3	11	·26
	110	5	23	79	4	14	·19	28	6	28	·26
	108	4	26	73	7	19	·10	21	5	21	·73
	68	3	24	72	6	25	·20	19	3	37	·67
	57	4	33	59	5	27	·28	15	3	10	·25
Mean 93	4	27	·34	76	6	20	·20	23	4	21	·43

C. fenestralis. Now Bristowe (1939) has suggested that with increasing size the 'athletic stamina' of spiders is impaired and the faster a spider runs the sooner it becomes 'tired out'. Millot (1949) also comments upon the poor stamina of spiders but suggests that this may be due to their imperfect circulatory system which allows blood to enter the pericardium without passing through the lungs. It seemed likely therefore that there might be a respiratory pigment in the blood with the function not only of an oxygen carrier, but also of an oxygen store, and that the greater 'strength' of *C. ferox* (Cloudsley-Thompson, 1954 a) might depend upon the presence of a proportionately larger respiratory surface which is correlated with a higher rate of water-loss by evaporation through the lung-books.

In order to test this hypothesis a number of experiments were carried out using all three species of *Ciniflo*. First, attempts were made to measure how long the animals could run at full speed before reaching exhaustion. It was difficult however to get an exact measure of exhaustion as, after a short sprint, some of the spiders continued plodding along slowly for some time whilst others resorted to death feigning. Nevertheless there was no doubt that when specimens of similar

size were compared, *C. similis* 'tired' more quickly than *C. ferox*. Possibly on account of their smaller size, the *C. fenestralis* could run at full speed for very much longer than either of the other species (Table IV). When supplied with oxygen all three species could maintain maximum speed for long periods.

TABLE IV.—Respiratory organs and water-loss in *C. ferox*, *C. similis* and *C. fenestralis*. N=number of specimens, m=mean, ‡=standard deviation. For further explanation, see text.

<i>C. ferox</i>			<i>C. similis</i>			<i>C. fenestralis</i>		
3-4 approx.			2-3 approx.			15-20 approx.		
<i>Time in minutes taken to reach exhaustion when running at full speed.</i>								
N 44	m 3	† 1	N 41	m 7½	† 2½	N 19	m 5	† 2
<i>Time in minutes taken to reach unconsciousness in ether vapour.</i>								
N 18	m 53	† 8	N 20	m 37	† 9	N 6	m 22	† 5
<i>Number of leaves in the lung-books.</i>								

In another series of experiments the time taken to reach unconsciousness in ether vapour was compared in the three species. This was investigated by placing a number of specimens of each species together in a crystallizing dish containing a pad of cotton wool moistened with ether and seeing which succumbed first. In these circumstances *C. ferox* invariably became anaesthetized before *C. similis* while the time taken by *C. fenestralis* was on the average intermediate between that of the other two (Table IV).

Finally the number of leaves in the lung-books of several specimens was counted under a binocular microscope. The morphology of the respiratory organs of spiders has been described in detail by Purcell (1909) and Kastner (1924), whilst Davies & Edney (1952) have shown that the tracheae are of negligible importance in respiration when compared with the lung-books and that the amount of oxygen that enters them is insufficient to keep a spider alive if its lung-books are blocked. Counting the number of leaves was by no means easy and consequently the figures given in Table IV may not be very accurate. In addition the number of leaves appeared to vary between different individuals. Nevertheless it was obvious that the respiratory area of *C. ferox* is considerably larger than that of *C. similis*, as suggested by the results of the experiments described above. It is therefore true to say that the greater 'strength', or rather 'stamina' of this species depends upon a proportionately larger respiratory surface acquired at the expense of greater dependence upon environmental humidity. That of *C. fenestralis* is probably correlated with its smaller size.

VI. RESPIRATORY PIGMENT.

The experiments described above indicate very strongly that an oxygen carrier must be present in the blood of *Ciniflo* spp. That haemocyanin is present as a respiratory pigment in the blood of spiders has long been suspected (Savory, 1928, etc.), but the evidence for this depends chiefly upon the fact that copper has been shown to be present in their tissues. For example, Griffiths (1893) found copper in the ashes of the spiders *Araneus* sp., *Tegenaria* sp. and *Pholcus* sp.: Muttkowski

(1921) showed that copper is distributed in all classes of Arthropoda, and Fox & Ramage (1931) found copper in all the tissues of the spider *Araneus diadematus* Clerck and *A. umbraticus* Clerck. Wilson (1901) had already concluded from the faint indigo-blue of the blood, which was decolorized with ammonium sulphide vapour and the presence of copper in the ashes of the spider, that haemocyanin was present in the blood of the large Egyptian spider *Chaetopelma olivacea* Koch, Deevey (1941) deduced the presence of haemocyanin in the Haitian tarantula *Phormictopus cancarides* (Latr.) from nitrogen and copper determinations of its blood. But apart from the serological experiments of Boyd (1937), which suggested that the serum protein of the Black Widow spider *Latrodectus mactans* (Fabr.) was chiefly or entirely a haemocyanin having about the same copper and nitrogen content as that of *Limulus* which it closely resembled serologically, there is no really conclusive evidence that haemocyanin is in fact the respiratory pigment of the Araneae, although there is considerable circumstantial support for the supposition.

My colleague Dr. L. G. E. Bell has therefore very kindly plotted for me the absorption curve of the blood from three female *C. ferox* diluted approximately 1 : 20 in Hilger 1 mm. silica cells, using a Hilger Uvispek spectrophotometer. The resulting curve (fig. 7) almost exactly compares with the absorption curves for crustacean, octopus and other well-known haemocyanins.

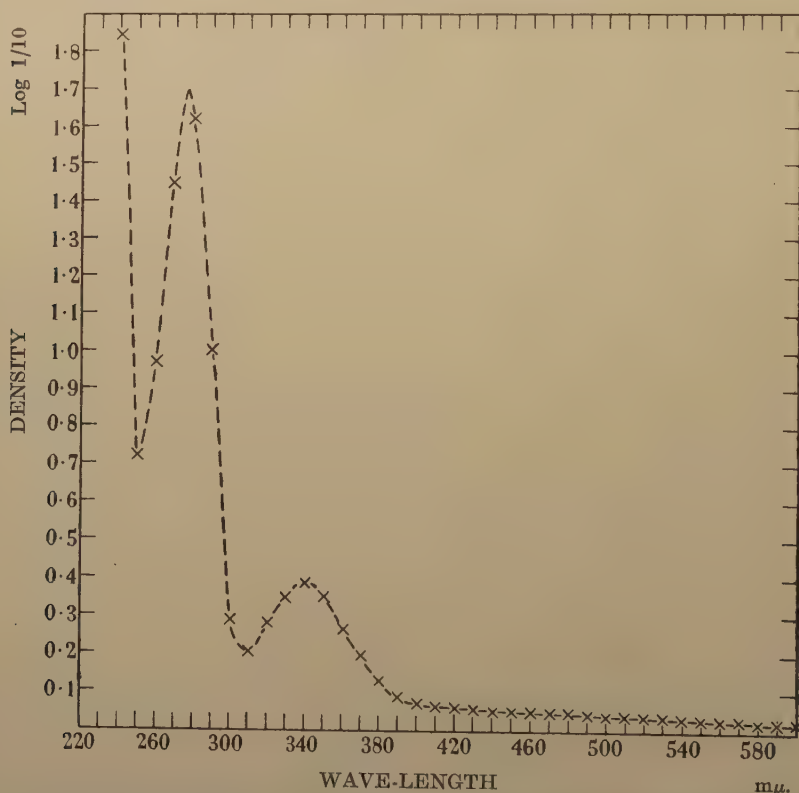


FIG. 7.—Absorption curve of blood of *C. ferox* measured by a Hilger Uvispek Spectrophotometer.

VII. HISTOLOGY OF THE INTEGUMENT.

(a) Lipoid staining.

A number of *C. ferox* were embedded in gelatine using Baker's Method (Pantin, 1946), sectioned with a freezing microtome, coloured with Sudan IV (Scharlach R.)

or Sudan black B and mounted in Farrant's medium. In such sections the very fine superficial layer of the cuticle which presumably corresponds with the epicuticle was deeply stained, while Sudan IV stained the exocuticle lightly as well. Krishnan (1953) obtained deep staining of the epicuticle in the scorpion *Palamneus swammerdami* (Sim.) with Sudan IV and concluded that a prominent chemical constituent of this layer was lipid.

(b) *Effect of lipoid solvents.*

Since the relative impermeability of the cuticle depends upon an epicuticular layer of lipid, it seemed probable that the removal of this by means of chloroform might result in an increase in the rate of water-loss in dry air, as occurs in the bug *Rhodnius prolixus* Stal., according to Wigglesworth (1945), and the millipede *Oxidus* (= *Paradesmus*) *gracilis* (C. L. Koch), according to Cloudsley-Thompson (1950 b). Batches of five *C. ferox* were therefore exposed to chloroform vapour and extracted with chloroform at different temperatures before their rate of water-loss over phosphorus pentoxide at 30° C. was measured. Half an hour was allowed to elapse after extraction to ensure that every trace of chloroform had evaporated before weighing. The results are presented in Table V, in which comparative figures for *Rhodnius* calculated from Wigglesworth's (1945) data and for *Oxidus* (from Cloudsley-Thompson, 1950 b.) are added. The figures indicate clearly that the water-proofing cuticular layer of *C. ferox* is removed much more readily than is that of *Rhodnius*, which is better able to survive desiccation and has greater powers of water retention. At the same time lipid is even less easily removed from *Oxidus* in which there is no critical point, although the exocuticle is impregnated with lipoids which reduce permeability (Cloudsley-Thompson, 1950 b).

TABLE V.—Loss of water in mg. cm.²/hr. at 30° C. from *Ciniflo ferox*, *Oxidus gracilis* (from Cloudsley-Thompson, 1950 b) and *Rhodnius prolixus* (data from Wigglesworth, 1945).

	<i>Ciniflo</i>	<i>Oxidus</i>	<i>Rhodnius</i>
A Dead, normal controls	0.2	3.0	0.0001
B After exposure to chloroform vapour at 20° C. for 1 hour	22.5	3.0	0.0009
C After extraction with chloroform for 15 minutes at 20° C.	39.0	3.0	0.13
D After extraction with chloroform for 15 minutes at 50° C.	57.5	10.7	1.7

The rate of water-loss below the critical temperature of *Ciniflo* spp. was very considerably increased after abrasion of the cuticle with inert alumina dust, as occurs in *Lycosa amentata* (Clerck), according to Davies & Edney (1952). Cloudsley-Thompson (1950 a) has shown that arachnids possess an epicuticular 'cuticulin' layer, and Sewell (1951) has demonstrated the presence of pore canals in the cuticle of spiders.

Thus the available evidence suggests that the integument of spiders, like that of other arachnids, is exactly comparable with that of insects (cf. Browning, 1942).

VIII. RESPONSES TO LIGHT, TEMPERATURE AND HUMIDITY.

The responses of spiders to environmental stimuli have not been studied to anything like the same extent as have those of insects. Millot (1946) however has recently reviewed the literature on the visual and chemical senses of spiders and a comprehensive bibliography, complete up to 1939, has been compiled by Bonnet (1945).

The aim of this part of my work has been merely to compare the intensities of the reactions of *C. ferox*, *C. similis* and *C. fenestralis* to those factors of the physical environment that might be expected to affect their natural distribution.

The temperature and light preferences of the spiders were investigated using standard choice-chamber technique (Cloudsley-Thompson, 1951 b, 1952 b). The apparatus comprised a number of glass arenas, each 10 cm. in diameter and subdivided into two halves by means of strips of metal but leaving sufficient space for the spiders to crawl unhindered beneath. The floor of each arena was composed of voile stretched over zinc gauze which in turn rested on damp filter paper. This maintained the relative humidity at almost 100 per cent on each side of the choice chamber, thus eliminating a difference in saturation deficiency that would otherwise have been caused by temperature differences between each half of the arena. Three spiders, one of each species, were placed in the arena and their positions noted at intervals of 15 minutes. The animals were stirred up with a glass rod after each reading and were changed after ten readings (2½ hours). The apparatus was rotated between readings so that the effects of any external factors were cancelled out.

In the first series of experiments the spiders were offered an alternative between darkness and the light from a mercury discharge lamp at 6 ft. distance (the intensity of this registered 6.5 units on a Weston Master II meter). Spiders moving after the 15 minutes had elapsed were not counted, while those within 1 cm. of the boundary were placed in a separate category and classified as 'Middle' in the final results which are expressed as percentages in Table VI.

TABLE VI.—Responses of *Ciniflo* spp. to environmental stimuli. Figures expressing percentages of spiders selecting the various alternative positions offered in the choice-chamber apparatus. For further explanation see text.

<i>C. ferox</i>			<i>C. similis</i>			<i>C. fenestralis</i>		
Dark	Middle	Light	Dark	Middle	Light	Dark	Middle	Light
69	10	21	63	18	19	76	13	11
<i>Reactions to light.</i>								
24° C.	Middle	19° C.	24° C.	Middle	19° C.	24° C.	Middle	19° C.
30	31	39	45	30	25	7	48	45
<i>Reactions to temperature.</i>								
100%	50%	0%	100%	50%	0%	100%	50%	0%
73	21	6	58	25	17	67	20	13
<i>Reactions to humidity.</i>								

In the second series of experiments a choice between temperatures of 19° C. and 24° C. was offered, spiders coming to rest within 1 cm. of the boundary again being placed in the 'Middle' category.

Finally it was found convenient to test the responses of the spiders to humidity over periods of 24 hours because they did not react quickly to this stimulus. A large oval arena measuring approximately 30 cm. in length and 10 cm. in breadth and having a height of 1 cm. was therefore constructed. Beneath the voile and gauze floor were three petri dishes: one of these contained calcium chloride crystals, the centre dish a mixture of sulphuric acid and water calculated to produce a relative humidity of 50 per cent and the dish at the other end, distilled water. Thus a gradient from 0–50–100 per cent relative humidity was produced and this was checked between

experiments by means of Edney paper hygrometers. Five spiders of each species of *Ciniflo* were placed together in the arena, which was covered with a glass plate. The apparatus was then covered to eliminate the light and next day the positions of the spiders within were noted. These were then either disturbed with a glass rod or replaced by fresh spiders whose positions were again noted after 24 hours. The results of a number of such tests extending over several weeks, expressed as percentages, are given in Table VI.

Blumenthal (1935) has shown that the 'tarsal organ' of a number of species of spider, including *C. fenestralis*, is a sense organ which responds to both humidity and smell. No significant difference was noted in the intensity of the responses of a number of spiders of all three species whose tarsi had been painted over with liquid paraffin.

The figures in Table VI indicate that the three species can be arranged in a series from *C. fenestralis* via *C. ferox* to *C. similis* as regards the intensity of their avoidance of light and temperature preference, *C. similis* being the least strongly photonegative and having the highest temperature preference. Finally *C. similis* is the least strong hygrotactic, followed by *C. ferox* and *C. fenestralis*. These results are not unexpected when considered in connection with the differing water-relations of the three species.

IX. DISCUSSION.

A number of authors have stressed the importance of atmospheric humidity on the ecology and distribution of spiders. For example, Weese (1925) showed that evaporation rate was one of a number of environmental factors that were of importance in determining the horizontal and vertical distribution of the spiders in an Illinois elm-maple forest. A few years later, Savory (1930) noticed that *Zygiella atrica* (C. L. Koch) builds its web in shrubs and bushes and shows a preference for moister air than does *Z. x-notata* (Clerck) which it resembles closely in size and general appearance but which builds its web on walls, window-frames in sheds and houses and in other drier places. Millot & Fontaine (1937) pointed out that some spiders such as the Lycosidae and Segestriidae need to drink, while others such as the Salticidae, Filistatidae and Thomisidae do not. They showed that the water content of the spiders of the former group was 70 per cent or more, while that of the latter group was less than 70 per cent and added: "Les *Amaurobius* appartiennent vraisemblablement à la première catégorie. . ."

Discussing the ecology and physiology of *Dolomedes fimbriatus* (Clerck), Palmgen (1939) explained the preference of this species for damp but unshaded places characterized by a luxurious growth of herbaceous vegetation as the result of positive phototactic and hygrotactic reactions while strong negative geotaxis explained its occurrence on the highest ground vegetation without accounting for its absence from trees. Lowrie (1942) showed that the low moisture content of the soil, the high temperature and duration of air movements were important factors restricting the distribution of spiders in the dry dunelands of the Chicago area. In a later paper (1948) he wrote: "Moisture in all its aspects is of prime importance to spiders", and he pointed out that soil moisture was of particular importance to ground-living species, especially burrowers.

Finally Nørgaard (1951) has investigated the ecology of *Pirata piraticus* (Clerck) and *Lycosa pullata* (Clerck) in a Danish sphagnum bog. He found that survival depended upon both temperature and relative humidity although curiously no preference was shown when a choice of different humidities was offered in an alternative chamber.

Probably insufficient time was allowed for the spiders to exhibit any preference, for it has been noted above (p. 148) that in the case of *Ciniflo* spp. several hours had to elapse before the animals responded to a humidity gradient and consequently experiments were carried out over periods of 24 hours. No doubt under natural

conditions the drinking of capillary water has considerable significance, for Parry (1954) has shown experimentally that *Tarantula barbipes* (Sund.) and *Lycosa radiata* (Latr.) can do so even against quite considerable suction pressures.

The present work again stresses the importance of moisture on the distribution of spiders. Differences in the physiology and ecology of the three species of *Ciniflo* can be explained almost entirely in relation to this one factor of the physical environment. In addition, however, attention is drawn to the conflict between the incompatible requirements of respiratory exchange and the prevention of water-loss, the relationship between which governs so much of the physiology of all the terrestrial Arthropoda. As far as I am aware, however, this conflict (discussed in Cloudsley-Thompson, 1955) has not previously been crystallized so clearly as in this study.

At the same time the different rates of water-loss through the lung-books of the three species can be correlated with differences in their responses to environmental stimuli: *C. similis* having greater powers of water retention and consequently less 'stamina' is the least strongly photo-negative and hygrotactic and has the highest temperature preference of the three species. No doubt the fact that *C. fenestralis* can run at full speed for longer periods than either of the other two species and yet has fewer lung-book leaves is due to its considerably smaller size.

X. SUMMARY.

This study represents an enquiry into the significance of the nocturnal habit in *Ciniflo ferox* (Walck.), *C. similis* Bl. and *C. fenestralis* (Stroem).

The validity of the generic name *Ciniflo* Blackwall is established.

Aktograph experiments indicate that all three species are nocturnal in habit and show a composite rhythm of movements and rest which is controlled primarily by alternating light and darkness, in the absence of which a rhythm can be set up by regular 24-hour cycles of temperature fluctuations. At the same time 18-hour cycles of light and darkness set up a weaker locomotory rhythm than that caused by 24-hour cycles. The intensity of nocturnalism is the same in all three species, over 90 per cent of their activity taking place during the hours of darkness.

When the water-relations of the three species are considered it is found that there is a critical temperature at approximately 35°C. above which all three species quickly lose water by evaporation in dry air, but below this *C. ferox* and *C. fenestralis* lose water more rapidly through their lung-books than does *C. similis*. As regards rate of water-loss through the lung-books, the species can be arranged in a series from *C. similis* through *C. ferox* to *C. fenestralis*, which shows the highest rate both in air of 50 per cent relative humidity and in dry air. The rate is almost doubled when 10 per cent of carbon dioxide is present, as this keeps the lung-books open. Conversely the time of survival in air of 50 per cent relative humidity and in dry air is longest in *C. similis* and shortest in *C. fenestralis*, death ensuing when from 20 to 25 per cent of total weight has been lost by evaporation.

C. similis 'tires' rapidly when forced to run at full speed without stopping, *C. ferox* less quickly, while *C. fenestralis* can maintain full speed for much longer. All three can run for long periods however when supplied with oxygen. *C. ferox* becomes anaesthetized most quickly in ether vapour, then *C. fenestralis*, while *C. similis* remains conscious longest. Finally *C. ferox* has the largest number of leaves in its lung-books, *C. fenestralis* least. The greater 'stamina' of *C. ferox* when compared with *C. similis* depends therefore upon a proportionately larger respiratory surface acquired at the expense of greater dependence upon environmental humidity. That of *C. fenestralis* is correlated with its smaller size.

It is shown that the respiratory pigment of the blood which acts as an oxygen store as well as an oxygen carrier is a typical haemocyanin, the absorption curve of which has been plotted. The histology of the integument is discussed: Sudan staining indicates the presence of an epicuticular lipid layer. Removal of this with chloroform greatly increases the rate of transpiration.

By means of choice-chamber apparatus it is shown that *C. similis* is less strongly photonegative than *C. ferox* and *C. fenestralis* and has a higher temperature preference. It is the least strongly hygrotaetic, followed by *C. ferox* and *C. fenestralis*. These results are not unexpected in view of the differing water-relations in the three species. Finally, the ecological significance of the physiological results obtained is discussed.

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THE EVOLUTION OF ARTHROPODAN LOCOMOTORY MECHANISMS.—
PART 5. THE STRUCTURE, HABITS AND EVOLUTION OF THE
PSELAPHOGNATHA (DIPLOPODA). By S. M. MANTON, F.R.S., from the
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(Natural History).

(With PLATE 5, and 8 text-figures.)

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INTRODUCTION.

It has been shown that for each of the major groups of Myriapoda so far considered (Parts 3 and 4) there is some particular habit of life which appears to have been of paramount importance in directing the morphological evolution of the group. The habit of pushing into the substratum by the motive force of the legs, together with that of rolling into a defensive spiral, probably led to the evolution of the diagnostic features of the trunk of the Diplopoda, including the diplo-segments. It has also been shown that effective burrowing in the diplopodan manner is only possible within a certain size range (see Part 4, p. 345). Attention has been drawn to millipedes outside this range; the larger Spirostreptomorpha are less efficient burrowers and have taken to speedier running and a more exposed habit, and it has been suggested that the differences in habit between *Blaniulus* and moderate sized Juliformia may

be associated with the former being near or beyond a lower limit of size for efficient burrowing by the bulldozer technique. The Pselaphognatha comprise only two families, the Lophoproctidae and Polyxenidae, and all are small, 4 mm. or less in length. The ring volume of *Polyxenus lagurus* is but one-third of that of *Blaniulus guttulatus*. The Pselaphognatha therefore might be expected to be well below the minimal size for efficient burrowing by pushing, and to differ in habits from other Diplopoda.

Structurally the Pselaphognatha stand apart from the rest of the Diplopoda (Latzel, 1884; Pocock, 1894; Verhoeff, 1901; Brölemann, 1935, and others), and there has been no clear interpretation of their morphology and relationships. Attems (1926) has suggested that "sie ein nahe der Wurzel des Diplopodenstammes abgezeigter Ast sind". Heathcote (1889) was inclined to regard *Polyxenus* "as an animal which has preserved certain traces in its anatomy of its descent from a common ancestor" of the Chilopoda and of the chilognath Diplopoda. Verhoeff (1901, 1926, etc.), in harmony with his view that the shortest bodied Myriapoda are the most primitive, supposed the Pselaphognatha to show the most primitive and "niedringster Organization" among Diplopoda. On the other hand, adherents of the opposing "Condensationsprinzip" regard these animals as specialized and not primitive. Reasons have been given in Parts 3 and 4 for the rejection of both these theories in their extreme form in favour of a middle course, but highly specialized features, such as the complex spines and mobile pleurites, are not far to seek in *Polyxenus*. An examination of the locomotory mechanism and habits of *Polyxenus* on the lines employed in previous parts might be expected to yield a measure of interpretation of structure on a functional basis, and to throw light on the phylogeny of the Pselaphognatha, and the results of such a study are given below. However, in many respects the morphology of this group has been but imperfectly and inaccurately described. In order to show the correlations which exist between structure and habits it has been necessary also to present a more detailed account of the skeleto-muscular system and of the cuticle.

HABITS OF MAJOR SIGNIFICANCE.

The manner of life of *Polyxenus lagurus* has been described most fully by Reinecke (1910) who reviews the earlier records. In Britain the most well-known haunts of this species are cracks leading deep into old stone and brick walls, among lichens and moss on walls and rocks, and under bark, but the animals have been found in places as diverse as sheltering among the roots of coastal plants (Blower *in lit.*), in the surface soil of woodland, and on the leaves of willows. *P. fasciculatus* occurs abundantly in the top few inches of soil in Duke's Wood, North Carolina (Starling, 1944). *Lophoproctus caecus* was collected under stones on a hillside in Italy (Pocock, 1894), and isolated specimens of a south American species of *Polyxenus* were found in soil crevices a foot below the surface by the Titicaca Expedition (H. Hinton *in lit.*). In common with other Myriapoda, the Pselaphognatha cannot withstand desiccation.

Polyxenus lagurus has been obtained for the present study mainly from old walls, where the animal occurs in small colonies, hanging on to the roof of extensive crevices which may be only just large enough for their entry, amid an abundance of cast skins. *Polyxenus* presumably returns to the same roosting places after excursions in search of food. Very few Diplopoda can walk upside down on a very smooth surface (see p. 167 and Part 4, p. 353) and none so expertly as *Polyxenus*, even ecdysis taking place in this position. In captivity this animal has chosen a glass ceiling rather than any other available place for roosting. *Polyxenus* is readily eaten by very small Isopoda, and Reinecke (1910) noted that spiders will eat *Polyxenus* but not other millipedes which are exposed in a dish. *Polyxenus* is not found in cracks large enough to admit spiders and isopods. By entering cracks as narrow as 0.5 mm. from floor to ceiling all arachnids with long pedipalps are avoided, and most predators capable of going into such places do not have long mouth parts

(see below). The ability to roost on a very smooth ceiling where predators may walk less easily must be advantageous. It may be suggested that taking refuge on the ceilings of crevices has been the habit of paramount importance in directing the evolution of the Pselaphognatha, other habitats being of secondary significance (see p. 183). For its size *Polyxenus* is fast moving (see p. 170), and it must often travel considerable distances from its hide in search of food or a bask in the sun when the air is damp.

The particular requirements of *Polyxenus* in respect of these habits would appear to be: adequate protection against predators and against drowning in the crevices which it inhabits, a narrow cleft may fill with water by capillarity or condensation, and when dry may be entered by minute isopods and mites; and a body construction and a locomotory mechanism conferring the ability to move, or to rest for long periods, on smooth surfaces inclined at any angle, together with moderate fleetness.

It will be shown below how the fulfilment of these present-day requirements, together with those of the supposed ancestors of the group, can account for the major trunk features of *Polyxenus*. Unlike other millipedes, *Polyxenus* does not push: a pushing habit would be incompatible with a soft integument, trichobothria on the head, loose joints, and the curious spines. Neither can it roll up.

TRUNK FEATURES WHICH RESEMBLE THOSE OF OTHER DIPLOPODA.

There is no doubt that *Polyxenus* is properly classed as a diplopod. The rings of the body are constructed basically on the diplopod plan, as are the arthrodial membranes between the tergites, the tracheal pouches, the basic plan of the musculature, the coxae of the legs closely approaching one another mid-ventrally, the head, the collum and the viscera.

In other Diplopoda the evolution of diplo-segments has been shown to be associated with the ability to push powerfully, and the presence of only one pair of legs on rings 2-4 or 2-3 enables a close protective spiral position to be assumed (see Part 4, pp. 348, 324 and 350). It may be suggested that the presence of both these features in *Polyxenus*, which neither pushes nor rolls up, is a legacy from primitive diplopodan ancestors which performed both these feats and had evolved these two characters.

TRUNK FEATURES WHICH DIFFER FROM THOSE OF OTHER DIPLOPODA.

An outstanding feature of the skeleto-muscular system and cuticle of the Pselaphognatha is the extreme lightness of construction. A ring of a juliform, a polydesmoid or oniscomorph millipede can be likened to a battleship or a bulldozer, with heavy exoskeletal plates and massive endoskeletal ridges for the attachment of bulky sheets of muscles (see Part 4). *Polyxenus* on the contrary resembles a toy glider made of linked struts of balsa wood and boxed in by tissue paper, with the muscles forming isolated bands between the skeletal units. Characters in which *Polyxenus* differs from Diplopoda of other orders are: the flatter shape; the smaller number of trunk rings; the greater power of telescoping one ring into the next and thereby shortening the body; the very thin uncalcified cuticle exhibiting unique features (see p. 174); the presence of trichobothria on the head and complex spines on the head and trunk; the form of the endoskeleton (see p. 158), a major part of which is in the form of a Y on the anterior face of the legs; the flexible sternites; the transference of the origin of the tracheal pouches from the sternites to the outer arm of the Y-skeleton; the form and immobility of the coxae and the staggering of the dorsal and ventral elements. All these features can be shown to be associated with the requirements mentioned above. An ability to resist longitudinal telescoping of the body by close-fitting ball and socket joints, necessary for a pushing habit in other Diplopoda, is not now required, and neither is the possession of a longish body with many rings, which in other Diplopoda provides a large pushing force from many legs (see Part 4, p. 345).

The anterior rings of most millipedes are smaller than those farther back, and the sternites of rings 2-4 may be very narrow, so allowing the assumption of a close spiral position (see Part 4, Pls. 54 and 55 and text-fig. 2 *d*). The anterior pedigerous rings of *Polyxenus* do not show these features, and it may be suggested that their absence is correlated with the loss of the spiralling habit. The pedigerous rings are more uniform in size, with a slight tapering of rings 1, 2, 8 and 9 (see Pl. 5). Consequently legs 1-3 are farther apart antero-posteriorly than are the remaining legs; the dotted lines on the right of text-fig. 5 *a* show the levels of origin of the legs, the distance between the origin of the 1st and 2nd pairs of legs, and the 2nd and 3rd pairs is the same as that between the 9th and 11th and 11th and 13th pairs.

GENERAL FORM OF THE RINGS AND JOINTS.

The cuticle of *Polyxenus*, unlike that of other millipedes, is nowhere rigid owing to the absence of calcification, but its basic structure is comparable to that of other Diplopoda except for modifications dependent perhaps upon its thinness (see p. 178).

The more rigid parts of each ring are: (1) A tergal half hoop shaped like an inverted 'U' and bearing two rows of complex spines. (2) A pair of small pleural plates, each situated on a lateral protuberance of the body and bearing a lateral rosette of complex spines. (3) The integument of the leg segments. (4) The Y-shaped skeleton on the front of each leg. (5) The homologue of the prophragma forming a thick rim along the anterior margin of the tergite. (6) Two pairs of tracheal pouches. (7) The internal U-shaped transverse tendons which are separate from the exoskeleton and segmentally arranged. (8) The horizontal V-shaped segmental struts fused to the transverse tendons. Elsewhere the integument is thinner and less resistant to deformation (see p. 178).

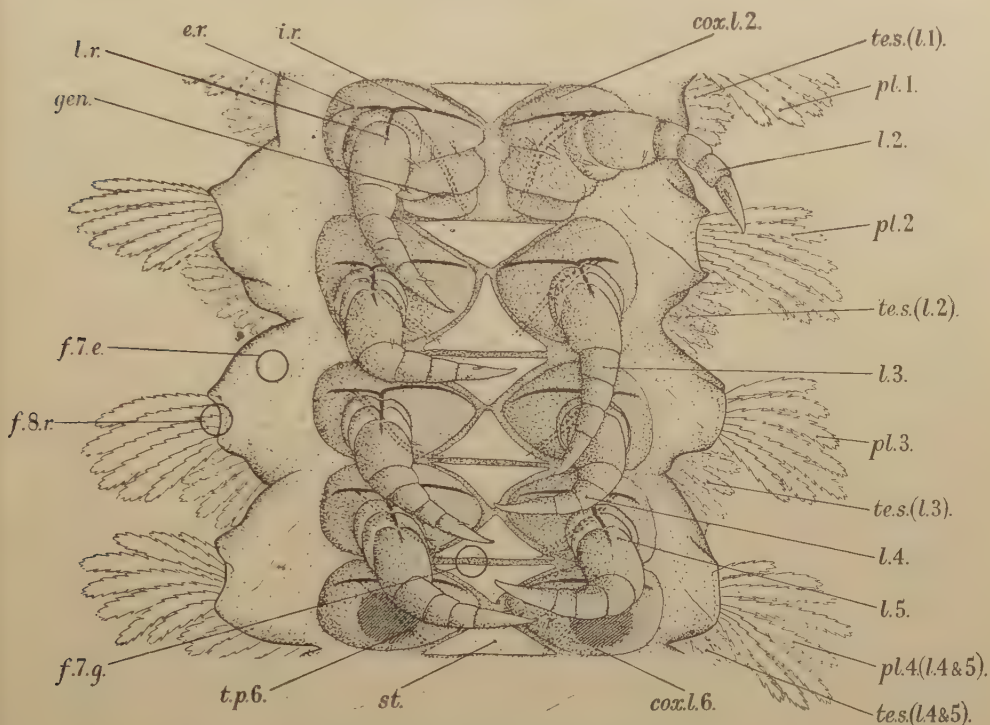
A non-telescopic inter-ring joint, so characteristic of the Diplopoda, is absent. Over the dorsal sector of the body the tergites overlap, and are united by simple arthrodial membranes (text-figs. 2 and 3 *b*), the detail being much as in Langner's (1937) fig. 20 of an oniscomorph, but there is no special joint across the ventral sector. The flexible lateral wall creases between the legs, and the flexible pedigerous lamina folds ventrally as shown in text-fig. 1.

In the Juliformia, Polydesmoidea, Nematophora and Colobognatha the legs of each ring are situated ventral to the tergite, whether the rigid parts of the ring are fused together or not (see Part 4, text-figs. 3 and 4), and this may be taken to be a primitive condition. In *Polyxenus* each pair of legs is displaced anteriorly relative to the tergite, so that the anterior pair lies below the tergite of the ring in front, see text-fig. 3 *b* where the legs and tergite of one ring are stippled, and text-fig. 1 which shows the positions of legs 4 and 5 (*l.* 4 and *l.* 5) relative to the corresponding pleurite *pl.* 4 (*l.* 4 and 5), and tergite spines *te.s.* (*l.* 4 and 5), and to leg 6 (*cox. l.* 6) which belongs to the succeeding ring.

The functional significance of this staggering is clear. In the absence of well-articulated inter-ring joints, maintenance of body shape and length is more dependent upon muscles, dorsal longitudinal, ventral longitudinal and dorso-ventral. Two paired groups of dorso-ventral muscles span each ring as shown in text-fig. 3 *b*, X and Y. The posterior pair of legs are linked to their tergite by muscles X, and the position of the anterior pair of legs allows them to be linked by muscles Y to the preceding tergite in a manner symmetrical with muscles X of the preceding ring. Successive rings are thus linked together in addition to the unions effected by the dorsal and ventral musculature.

Reference has been made in Part 4 to the complex staggering and overlapping of the tergites, pleurites, sternites and legs of the Oniscomorpha. The sternites are displaced forwards relative to the pleurites (see stippled parts in text-fig. 4 *c*, Part 4) and the posterior pair of legs of each ring lie below the anterior part of the succeeding tergite, representing a shift in the opposite direction to that of *Polyxenus*. The functional significance of the staggering of the Oniscomorpha differs from that of

Polyxenus. The oniscomorph condition is associated with the compression of the ventral elements when the animals roll up. The head crowds the legs mid-ventrally, and the legs crowd each other and pack into the space *slc.* shown in text-fig. 4 *a*. Part 4, the backward shift of the leg-origin facilitating this compression. Anteriorly the sternites find space at the side of the head in the rolled-up position, and the forward overlapping of the sternites fixes the transverse axis of dorso-ventral bending



TEXT-FIG. 1. (Key to lettering p. 186).

Ventral view of *Polyxenus lagurus* showing the disposition of the stiff (mechanically stippled) and soft (white) integument, and the forward displacement of the legs of each ring. Legs, pleural spine rosettes and tergal spines belonging to one ring are numbered to show their correspondence.

low down (see Part 4, pp. 317, 352, 368). Thus the contrasting staggering of the ventral parts of the Oniscomorpha and Pselaphognatha are both associated with different functional needs and both may be regarded as independent specializations.

PROVISIONS FOR DEFENCE.

A slight dorso-ventral flattening of each ring (the $\frac{\text{depth}}{\text{width}}$ is about 0.6–0.7*, see Pl. 5) enables the animal to fit more closely into a narrow cleft than would a diplopod with a cylindrical body. The anterior row of tergal spines is directed outwards, almost in the transverse plane. In a narrow crevice many spines may touch the roof, so that the body and spines span the gap completely. This flattening of the rings does not impede inter-ring mobility in the horizontal plane (see Pl. 5, fig. 10) where the degree of flexure corresponds to those of Juliformia with com-

* Measured from living animals;

parable ring shapes. The $\frac{\text{width}}{\text{length}}$ of the rings* of *Ophistreptus*, *Polyxenus* and *Tachypodiulus* are about 5, 3+ and 3 respectively, and their maximum angles of horizontal flexure are about 13°, 15° and 16°.

A protective function has been ascribed to the spines by Latzel (1884), Reinecke (1910) and others, both for the adult, and for the eggs which are covered by spines from the parent. The inter-ring joints are loosely constructed, and consequently telescoping at the joints can occur, allowing a shortening of 22 per cent of the fully extended running length. This shortening brings the posterior row of tergal spines, which are directed almost parallel to the body surface, close up to the anterior row of tergal spines of the following ring (Pl. 5), so covering the body surface with a pallisade of stiff and heavy armature. The pleural rosettes are also brought close together, the anterior spines of each rosette overlapping the posterior spines of the rosette in front rather more than is seen on Pl. 5, fig. 11, right side. When thus encased the rings cannot flex on one another so easily and the legs are crowded. This protective telescoping takes place when ever locomotion ceases, and re-extension occurs when the animal walks.

In a narrow crack just large enough to take *Polyxenus* the animal is very well protected. The tergal spines meet the roof as well as each other, and the head spines, nine pairs of pleural spine rosettes and the paired tail bundles protect the flanks. Laterally the two tergal spine rows are united by a fan of spines, and owing to the forward displacement of the pleural rosettes the lateral tergal fans alternate with the rosettes, so closing the gaps between them. These long serrated spines keep predators small enough to enter the crack at 'arms length' and away from the actual body surface. Muscles move both tail bundles and lateral rosettes (see pp. 163 and 164 and Reinecke, 1910).

The forward extension of the pleurite of ring 2, bringing the first spine rosette level with the spines of the collum (Pl. 5), and the position of the 9th rosette are such that the full range of limb positions of all the legs is covered by the spines (text-fig. 5 a and Pl. 5, figs. 12 and 13).

The spines of *Polyxenus* serve another purpose. Besides the large complex spines the whole surface of the body and legs is clothed with minute simple spines, a condition found in no other diplopod. Minute sculpturings and spines also cover the surface of *Peripatus* and the *Symphyla*, and all these animals show great resistance to wetting. Both large and small spines in *Polyxenus* are hydrofuge (see p. 178) and may prevent drowning if water invades the hide, the large air-filled spines keeping water away from the body and the small spines preventing wetting if the outer defences become penetrated. The retention of air round the animal may also have a respiratory significance. Reinecke (1910) has remarked on the manner in which the large spines prevent *Polyxenus* from sinking when immersed in water (see also pp. 178 and 179).

THE SKELETON.

The most striking features of the skeleton concern the elaborate yet light devices which maintain the immobility of the coxa and give rigidity to the Y-shaped leg skeleton; both are essential requirements for the precision of action of intrinsic and extrinsic leg muscles which enables *Polyxenus* to walk upside down on very smooth surfaces.

In Diplopoda other than the *Pselaphognatha* each paired or median sternite carries the corresponding tracheal pouch or pouches and with them forms a rigid unit, whether the sternites are fused with other parts of the ring or not. The spiracle perforates the sternite just lateral to the leg base. The coxa of the leg is movably articulated with the sternite-tracheal pouch unit; there is great variety in the

* Measured from living animals.

nature of this articulation, the head of the coxa may be narrow (Juliformia) or wide (Cologbognatha); it may be surrounded by the sternite (most Diplopoda) or hinged to it on one side only (Oniscomorpha) (see Part 4, text-figs. and Silvestri, 1903). Extrinsic protractor and retractor muscles run from the tracheal pouch to the coxa (and sometimes to other leg segments also): the coxa swings backwards and forwards, but no levator or depressor movements are possible (see Part 4, pp. 311, 314, etc.). Ventral longitudinal muscles run between successive tracheal pouches on either side.

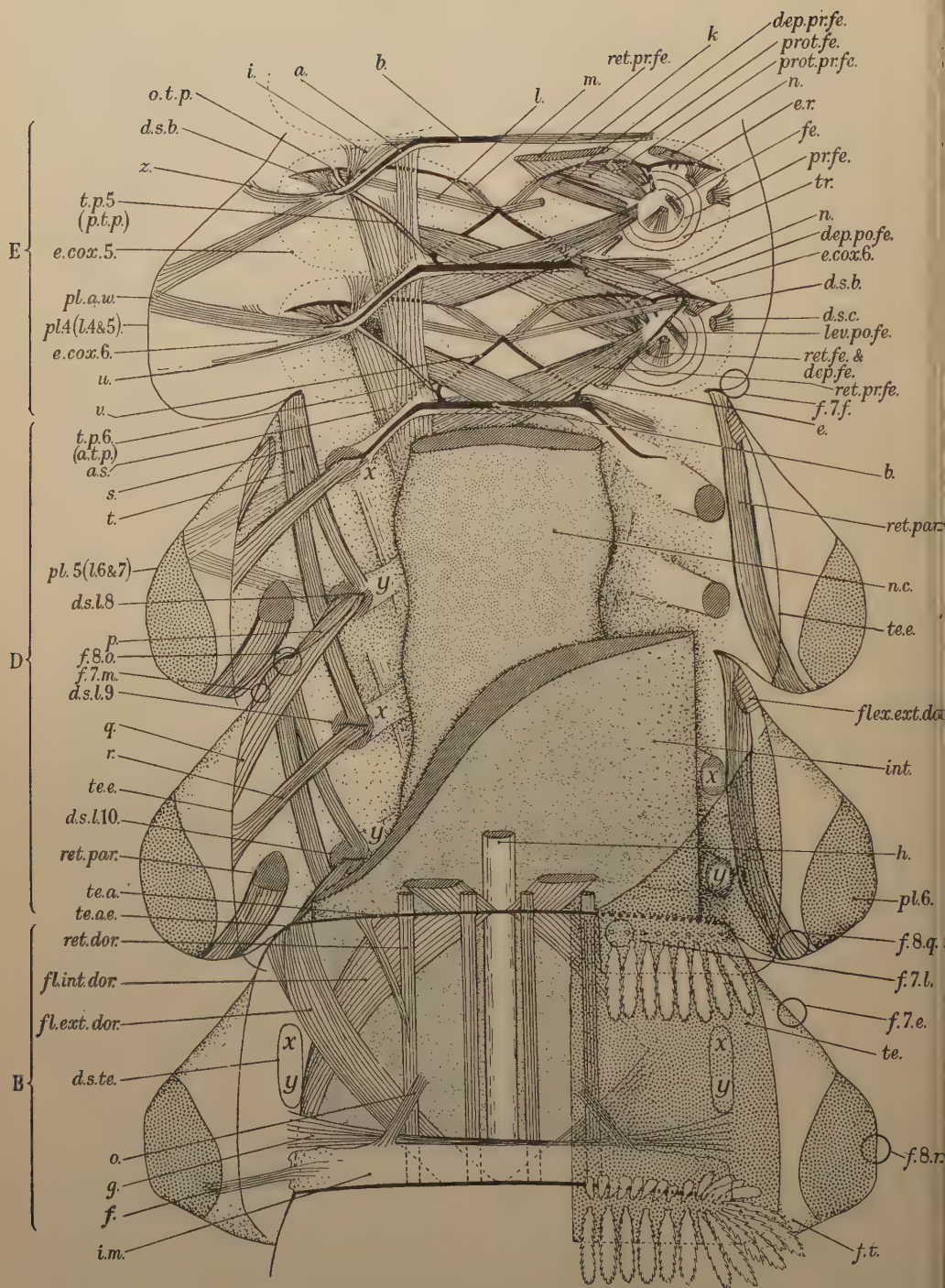
In *Polyxenus* the coxa is short, wide and almost bun-shaped (text-fig. 1, *cox. l. 2, cor. l. 6*). It approaches its fellow in the middle line and successive coxae in front and behind. Unlike all other millipedes the coxa is not independently movable. Its proximal rim is not nicely articulated with a rigid part of the ring, but is surrounded by the flexible pedigerous lamina which folds as shown in text-fig. 1. Two soft triangular areas lie across the middle line between each pair of legs and are separated by shallow grooves, the integument being similar both in the folds and on the flat parts of the lamina (text-fig. 7 *g*). Each triangular zone must represent the anterior or posterior part of a median sternite as seen in other Diplopoda, but these triangles do not reach the lateral side of the leg, and they do not carry the tracheal pouches. The spiracles in *Polyxenus* are situated in the normal diplopod position relative to the movable part of the leg, but they arise from the outer arm of the Y-shaped skeleton and not from sternites.

The *Y-shaped leg skeleton* has been described and figured in part by Silvestri (1903, fig. 214), Reinecke (1910 text-fig. 14) and Verhoeff (1929). This skeleton is an inwardly projecting chitinous ridge on the exoskeleton. It lies across the front of the coxa, and extends down the anterior face of the trochanter, prefemur and proximal part of the femur (text-figs. 1 and 3 *A, e.r., i.r. and l.r.*). The stem of the Y is hinged at the joints between the leg segments, and lateral ribs run out from it along the margins of the segments, as shown most clearly on the left side of text-fig. 3 *A*. Since each tracheal pouch and Y-shaped skeleton form one unit, no movement is possible between the coxa and the tracheal pouch. A nicely formed articulation between the coxa and the ring is not required, and the usual diplopodan extrinsic muscles from the coxa to the tracheal pouch are absent (see p. 166). Verhoeff (1929) has remarked: "Alle diese Spangen sind eine Anpassung an die für Diplopoden ungewöhnlich dünne und Schwache Chitinhaut . . . sie dienen einerseits einem Teil der Beinmuskeln zum Ansatz und ersetzen anderseits auch die Sternite, weil dieselben bei den Pselaphognathen nur häutige Kissen vorstellen . . . Es zeigt sich aber ein mechanischer Sternitersatz auch darin, dass das äussere Ende der Trachentaschen . . . an den äusseren Ast der Querspange anlehnt".

The *tracheal pouches*, which lack an outer arm, are directed posteriorly and towards the middle line as shown in text-figs. 1, 2 and 3, where they end just internal to the lateral angles of the sternites and close to the nerve cord, each pair uniting with a segmental transverse tendon. Only in shrunk specimens do the tracheal pouches cross each other, as figured by Silvestri (1903, etc.).

The *transverse segmental tendons*, chitinous and separate from the exoskeleton, correspond in number to the paired legs. Each tendon is U-shaped, the middle of the bar being situated below the nerve cord and above the posterior part of a pair of coxae (text-fig. 3 *A* and *B, b*), while the arms *a* pass upwards and backwards to associate with muscles from the legs behind (text-figs. 2 and 3). Latero-ventrally the tendons unite with the inner ends of the tracheal pouches from the legs in front, as shown in text-figs. 2 and 3 *A*.

These tendons are homologous with those of the mandibular adductor muscles of most Arthropoda *vera*, and with the segmental ectodermal tendons of Crustacea which are elaborated into endoskeleton or smaller unions between the paired meso-



TEXT-FIG. 2. (Key to lettering p. 186).

Reconstruction of *Polyxenus lagurus* in dorsal view to show the skeleto-muscular systems. The tergal surface is shown in A, and structures are cut away at successively deeper levels in parts B-F. The lateral limit of the diagram in F represents the body wall below the pleural lobe. The viewpoint is slightly oblique in order to display certain muscles; the segmental endoskeletal bars in E and F are actually above the posterior edge of the preceding coxae, as shown in text-fig. 3 b. Endoskeleton is shown in black. Circles indicate position of sections shown in text-figs. 7 and 8.

dermal muscles (Manton, 1928, text-figs. 15, 22, 23, Pls. 23 and 24, figs. 18 and 27 and 1934, text-figs. 7, 14, 15 and 17). The tendons in *Polyxenus* differ from those of the known Malacostraca in being situated below and not above the nerve cord. No such tendons have been found in the trunk region of the armoured Diplopoda, where indeed they are not required. It may be suggested that the occurrence of these tendons in the Pselaphognatha represents the exploitation of a basic arthropodan potentiality in respect of present needs, and with the units mentioned below, maintain the necessary rigidity in the absence of the usual heavy components of diplopod endo- and exoskeleton. In Crustacea these tendons arise from the embryonic intersegmental ectoderm, and they doubtless arise in a similar manner in *Polyxenus*, but have become less far removed from the surface in the vicinity of the nerve cord, and the base *b* has presumably swung a little forward while the arms *a* have tilted backwards.

A V-shaped bar of chitin lies horizontally in front of each tendon, the arms of the V being fused with the tendon at its union with the tracheal pouches (text-fig. 2, *v*). The apex of the V lies close under the nerve cord and slightly more dorsal than the middle part of the segmental tendon (the V-shaped bar is displaced in the diagram of text-fig. 3 *A* for the convenience of showing the muscles).

A rigid lattice of six components is thus formed by the Y-shaped skeleton and tracheal pouches of each pair of legs united behind to a segmental tendon and to a V-shaped bar. All parts stain dark blue with Azan. Each lattice can approach or recede from adjacent units. The span of each lattice from the anterior part of one pair of coxae to above the middle of the succeeding pair allows muscles from three leg-bearing segments to control the position of each coxa and Y-shaped skeleton.

THE TRUNK MUSCULATURE.

The muscles of *Polyxenus*, although based upon the diplopod plan, are as strikingly different from the muscles seen in other diplopod orders as is the skeleton. Broad sheets of muscles (see Part 4, text-figs. 3, 4 and 8) are replaced by slender penicilli, and many new muscles are associated with stabilizing the trellis-like endoskeleton, the immobile coxae and the provision of extrinsic leg muscles inserted on to the prefemur instead of on to the coxa (text-figs. 2 and 3).

The muscles of *Polyxenus* have been described by Silvestri (1903), but the meticulous accuracy which characterizes most of this monograph is here marred, and the description relating to *Polyxenus* suffers from too much incompleteness and fundamental misinterpretation to serve the present purpose. An outline is therefore given below of the principal muscles of *Polyxenus*. In Part 4 Silvestri's original terminology for muscles was adopted for all muscles previously described. For *Polyxenus* Silvestri's terminology is used below only for those muscles in which he correctly indicated the function and position.

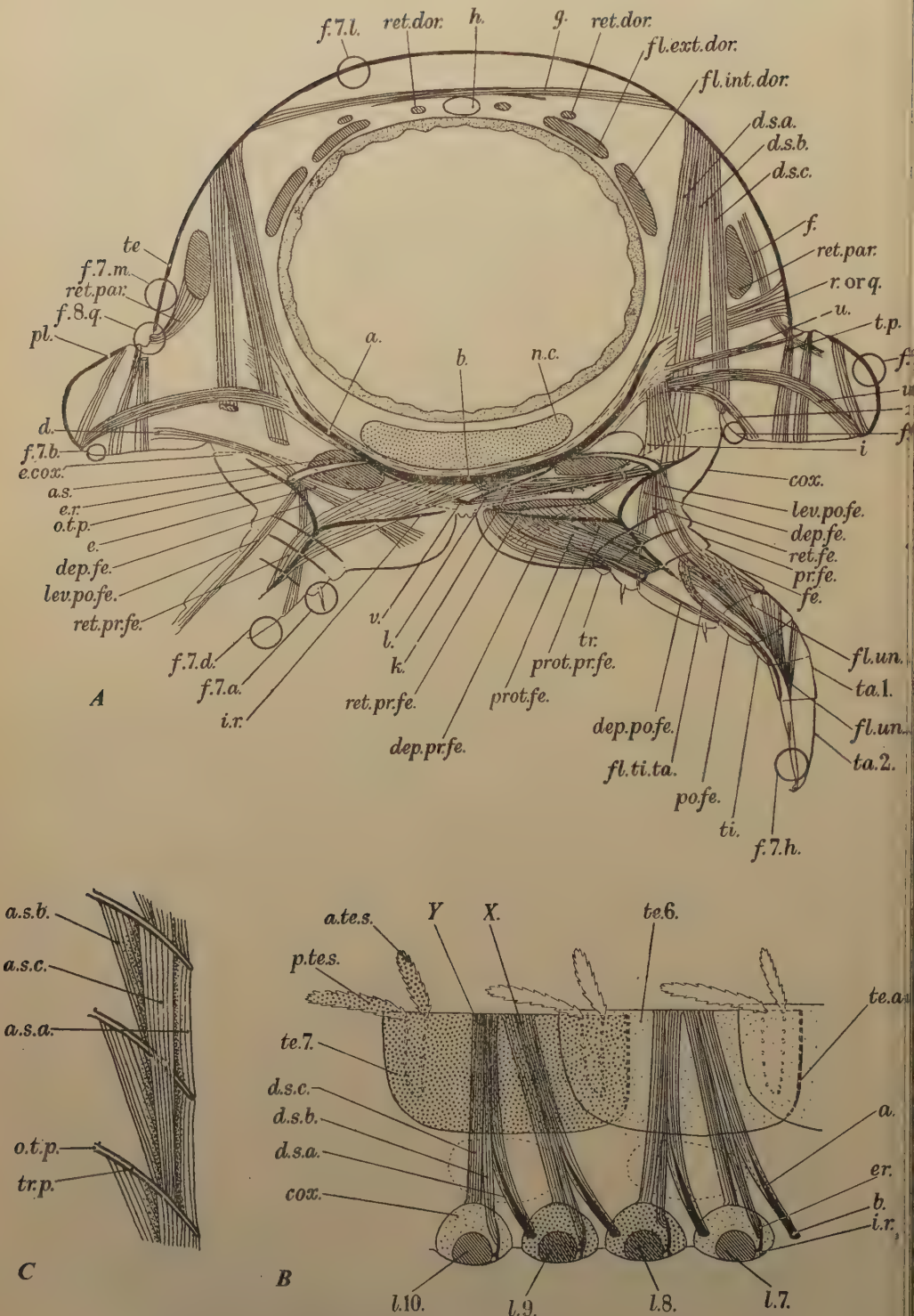
Muscles which are directly comparable to those of other Diplopoda.

Retractor dorsalis. Two pairs of small strands run dorsally between the anterior rims of one tergite and the next, *ret.d r.*, text-figs. 2 and 3 *A*.

Flexor externus dorsalis runs from the lateral end of the anterior rim of the tergite to the sub-median part of this rim on the following tergite, *fl.ext.dor.*, text-fig. 2.

Flexor internus dorsalis runs from the sub-median part of the anterior rim of the tergite to the lateral edge of this rim on the following tergite, *fl.int.d.r.*, text-fig. 2.

Retractor paratergalis runs from the antero-lateral edge of the tergite backwards and slightly downwards to the flexible integument between tergite and pleurite on the posterior side of the pleural lobe of the same ring, *ret.par.*, text-figs. 2 and 3 *A*.



TEXT-FIG. 3. (Key to lettering p. 186).
 Circles indicate position of sections shown in text-figs. 7 and 8.

M. apophysis sternalis is complex in structure (text-fig. 2, *a.s.*). Strands run between the inner ends of successive tracheal pouches, inserting also on to the segmental tendons; other strands from the outer posterior side of a tracheal pouch run obliquely inwards and backwards to the inner anterior face of the succeeding tracheal pouch, while some fibres from the middle of a tracheal pouch pass backwards crossing over the next tracheal pouch to insert upon the following one (see text-fig. 3 C, *a.s.a.*, *a.s.b.* and *a.s.c.*). It is possible that some fibres extend for greater distances before uniting with the main complex.

Trunk muscles which are peculiar to Polyxenus.

Two groups of *dorso-sternal muscles* insert on to the tergite on either side in the rings which bear two pairs of legs. Only one paired group is found in the anterior rings bearing one pair of legs. These groups, X and Y in text-figs. 2 and 3 B, are each composed of three muscles. The anterior and inner muscle *d.s.a.* passes to the arms *a* of the transverse segmental tendon; the middle muscle *d.s.b.* passes down to the outer arm of the Y-shaped skeleton and the outer and most posterior of the group, *d.s.c.*, runs to the lateral edge of coxa.

Lateral tergo-sternal muscles from the arms *a* of the transverse segmental tendons run outwards to the lateral edges of the tergites (text-figs. 2 and 3 A). From the transverse tendon associated with dorso-sternals X a muscle *r* runs outwards and backwards to the middle of the lateral edge of the tergite, and another *t* runs forward to the antero-lateral corner of the preceding tergite. From the transverse tendon associated with dorso-sternal muscles Y a muscle *s* runs forwards to the antero-lateral edge of the tergite, another *q* runs outwards and backwards to the middle of the lateral edge of the succeeding tergite and a third muscle *p* runs backwards and outwards to the lateral corner of the rim along the front of the succeeding tergite.

From the arms of the transverse segmental tendons and just below the origin of the tergo-sternal muscles paired *pleuro-sternal muscles* pass out laterally and latero-ventrally into the pleural lobe. The main pleuro-sternal muscle *w* (text-fig. 3 A) extends through the middle of the pleural lobe, and the muscles *w* from the two segmental tendons in each ring converge on to the lower edge of the pleurite in a symmetrical manner (*pl.a.w.* in text-fig. 2). Only one such muscle supplies each pleurite of rings 2-4 which bear one pair of legs, and the single muscle *w* then runs transversely and not obliquely through the middle of each pleural lobe. From the tendon associated with dorso-sternal muscles Y a smaller muscle *u* passes into the posterior part of the pleural lobe, inserting on the flexible cuticle

TEXT-FIG. 3.

For key to lettering see p. 186.

Reconstructions of *Polyxenus lagurus* to show the skeleto-muscular systems.

- (a) Diagrammatic anterior view of the body and legs. Tergite, pleurites, transverse segmental tendon, tracheal pouches, Y- and V-shaped skeletons are shown in black. The V-shaped skeleton projects anteriorly in front of the transverse tendon, the apex lying close to the nerve cord (see text-fig. 2), but has been distorted here in order to include it in the diagram. Muscle *l* is shown, but reference must be made to text-fig. 2 to ascertain to which leg and V-shaped skeleton it is attached. Protractor leg muscles are shown on the right. The retractor pre-femoris on the left lies on the posterior side of the leg, the Y-skeleton being situated on the anterior face.
- (b) Lateral view of two diplo-segments. The coxae of legs 8 and 9 and their corresponding tergite are stippled. The pleurites and their muscles are omitted. They lie roughly opposite the dorso-ventral muscles X and Y, dotted line. The segmental transverse tendon and Y-shaped skeleton are shown in black.
- (c) Diagram in dorsal view of the ventral longitudinal musculature (musculus apophysis sternalis *a.s.* in text-fig. 2) of the left side to show three component parts.

between tergite and pleurite (text-figs. 2 and 3 A). Another muscle *z* from each segmental tendon runs downwards and outwards, just anterior to muscle *w* to insert on the soft ventral pleural wall as shown in text-figs. 2 and 3 a. A small muscle passes into the pleural lobe ventrally, arising from the tracheal pouch near its external opening *d* in text-fig. 3 A.

Tergo-pleural muscles run in several directions. The lower edge of the tergite is tied to the ventral side of the pleural lobe by several separate muscle strands, one being shown, *t.p.* in text-fig. 3 A. and the folds of the inter-tergite arthrodial membrane are tied laterally to the pleural lobe by muscle *f* in text-figs. 2 and 3 a.

Several dorso-ventral and oblique *pleural muscles* span the pleural lobe. Two of these are shown in text-fig. 3 A, unlabelled.

Muscles to the arthrodial membrane between the tergites comprise three pairs. The muscle *f* to the pleural lobe has been mentioned above; muscle *o* obliquely ties the membrane to the tergite in front as shown in text-fig. 2 and muscle *g*, arising from the tergite behind the insertion of the dorso-sternal muscles, passes transversely, crossing its fellow, to the membrane on the other side of the middle line (text-figs. 2 and 3 A).

One pair of *muscles to the pedigerous lamina* is inserted where the lamina is narrowest in the fold between successive legs, and runs transversely towards the middle line to insert on the median basal part of the segmental tendon (*k* in text-figs. 2 and 3 A, and also see text-fig. 1).

Paired *muscles to the V-shaped skeleton* form a zig-zag series lying almost in the horizontal plane. From the arms of the V, where they unite with the segmental tendon, muscle *n* passes outwards and backwards to the outer arm of the Y-skeleton of the leg behind. From the apex of the V a short muscle *m* runs forwards to the inner arm of the Y-skeleton of the leg in front, and a longer muscle *l* runs forwards and outwards to the outer arm of the same Y-skeleton (text-fig. 2).

Muscles which move the posterior bundles of setae.

Each bundle of posterior spines is situated on a dorso-lateral lobe of the telson, and each is moved principally by one intrinsic and two extrinsic muscles. Dorsally the retractor dorsalis of the 10th ring inserts on the anterior margin of the telson, and dorso-laterally the retractor paratergalis of the 10th ring inserts posteriorly mainly upon the posterior spine-bearing lobe on each side, only a few strands passing to the pleural lobes of the 10th ring, as on other rings. A considerable part of the internal space within each lobe is occupied by a large dorso-ventral muscle, and in addition there are a few small oblique strands.

Muscles of the leg segments.

Muscles to the coxa. Besides the dorso-sternal *d.s.c.*, two other muscles are inserted on the margin of the coxa. Muscle *i* (text-figs. 2 and 3 A) leaves the antero-lateral margin of the coxa, and passes almost vertically upwards to the lateral arm of the transverse segmental tendon. Muscle *e* leaves the posterior margin of the coxa a little farther towards the middle line than is shown in text-fig. 2, where the muscle is complete on leg 6 and cut short on leg 5. Muscle *e* is more accurately shown in text-fig. 3 A; it inserts upon the tracheal pouch near the external opening. (For homologies see p. 166).

Muscles to the pre-femur number four and form the main extrinsic muscles causing stepping. The *retractor pre-femoris* is very long. It originates mainly from the

postero-ventral edge of the prefemur, some fibres arising from the corresponding part of the femur. This large muscle passes mainly to the middle of the segmental tendon, some strands crossing over to the other side and inserting onto the anterior face of the inner arm of the Y-skeleton of the leg behind on the opposite side. The muscle interdigitates with its fellow in the middle line (see *ret.pr.fe.*, text-fig. 2), the two ends of the muscle being shown in text-fig. 3 A. A short stout muscle (not shown on the figures) leaves the prefemoral origin of the retractor and passes upwards outside the tracheal pouch to the main lateral muscle complex. *Protractor pre-femoris* is short, running from the anterior edge of the pre-femur forwards to the inner ramus of the Y-skeleton *prot. pr. fe.* text-figs. 2 and 3 A) near the stem of the Y. A *depressor pre-femoris, dep.pr.fe.*, extends from the mesial side of the pre-femur inwards and forwards to the tip of the inner ramus of the Y-skeleton.

Muscles to the femur. From the proximal mesial face of the femur the *depressor femoris* passes directly upwards to the outer end of the tracheal pouch. Lateral to this muscle the *retractor femoris* leaves the posterior distal face of the femur and runs to the outer end of the tracheal pouch (*dep.fe.* and *ret.fe.* in text-figs. 2 and 3 A).

Muscles to the post-femur. A *levator post-femoris, lev.po.fe.*, lies directly external to the retractor femoris. It leaves the distal side of the dorsal hinge between post-femur and femur and runs upwards to the outer end of the tracheal pouch close to the spiracle, traversing the femur, pre-femur, trochanter and coxa (text-fig. 3 A). A *depressor post-femoris* leaves the mesial proximal edge of the post-femur and passes inwards and upwards to the inner ramus of the Y-skeleton internal to the depressor femoris and protractor pre-femoris. The distal part of this muscle, *dep.po.fe.*, is seen in text-fig. 3 A and the proximal part on right leg 6 in text-fig. 2, the muscle being partly cut away on right leg 5 in this figure.

Muscles to the tibia, tarsus 1 and tarsus 2. Only one muscle supplies these segments. *Flexor tibiae-tarsi* leaves the proximal mesial edge of tarsus 2, uniting with fibres from the corresponding points of tarsus 1 and tibia, and runs upwards to the posterior proximal face of the femur (*fl.ti.ta.*, text-fig. 3 A).

Muscle to the tarsal claw. The apodeme from the mesial side of the claw (*a.c.* text-fig. 4 b) extends into the distal part of the post-femur. *Flexor unguiculi* from this apodeme sends one strand dorsally to the proximal part of the tibia, a large set of strands inserts dorsally on the proximal half of the post-femur, and a bulky mass of muscles fans out dorsally and laterally over most of the femur (*fl.un.*, text-fig. 3 A).

THE MODE OF ACTION AND THE EVOLUTION OF THE TRUNK SKELETO-MUSCULAR SYSTEM.

The detailed morphology of the endoskeleton is unique among millipedes, yet it appears to be a derivative of the basic diplopod pattern. It may be suggested that reduction in the exoskeleton was accompanied by the evolution of the particular lattice of endoskeletal bars found in *Polyxenus* and by a secondary shift in origin of the tracheal pouches (see above, pp. 155 and 158). There is no indication that the soft integument (see p. 180) or the peculiar endoskeleton represent a primitive diplopodan condition; both are suggestive of specialization. The mode of action of the skeleton will be considered below together with that of the muscles.

The functions and homologies of the muscles have been indicated to some extent above by the arrangement of their diagnoses, but there are further points of interest.

The limited degree of lateral bending between the rings is mediated, as is usual in diplopods, by the crossed flexor muscles.

Longitudinal cohesion between the rings is effected by the unusually weak retractor dorsalis, by the strong apophysis sternalis complex and by the paratergalis. The latter is large, and unusual in being confined to one ring; its posterior insertion however must pull indirectly both on the succeeding tergite and on the whole posterior part of the cushion-like pleural lobe, so making room for the telescoping of the tergites.

The antagonists of the three longitudinal muscles must be the dorso-sternals, tergo-sternals and pleuro-sternals, all attached to the transverse segmental tendons: contraction of these muscles must cause elongation of the body. The folding of the pedigerous lamina, with muscles *k* which keep the folds in place (text-figs. 2 and 3 A), must facilitate the alternate telescoping and elongation of the body. Elongation and contraction of the body of *Polyxenus* is advantageous (see p. 158), although such movements must be avoided by most millipedes, and are in fact prohibited by their skeleto-muscular specializations (Part 4, pp. 303-4).

Reference has already been made to the linking together of successive rings by the staggering of the dorsal and ventral elements and the consequent association of the X and Y groups of dorso-sternal muscles. The trellis-like arrangement of the lateral tergo-sternal muscles *p*, *q*, *r*, *s* and *t* (text-fig. 2), linking every transverse U-shaped tendon with two tergites, must control the positions of the arms *a* of the successive tendons, while the ventral longitudinal muscles *a.s.* stabilize the bases *a* of these tendons.

The general form of the complex ventral longitudinal muscles shows a remarkable convergence to the muscles of other Myriapoda possessing a considerable amount of flexible ventral body wall. The muscle strands *a.s.a.*, *a.s.b.* and *a.s.c.* (text-fig. 3 C) of *Polyxenus* are analogous to the oniscomorph complex shown in Part 4, text-fig. 8, p. 354, *ret.par.*, *fl.in.long.ex.* and *fl.in.long.in.* which is formed by the retractor paratergalis and flexor inferus longus muscles. The Symphyla possess small isolated sternites roughly resembling the coxae of *Polyxenus*, and the main ventral longitudinal muscle runs from the basal part of one apodeme obliquely backwards to the tip of the following apodeme (see Tiegs, 1940 and a subsequent Part), very much as do the oblique components of *Polyxenus a.s.b.* and the *fl.in.long.ex.* and *fl.in.long.in.* *Sphaerotherium*. These similarities suggest that the possession of some muscles set obliquely is more suited to holding together loosely articulated elements than would be straight sheets of muscles running directly between corresponding segmental insertions on the hard parts. The ventral muscles of most diplopods are of the latter type and run directly from corresponding segmental points (see the musculus lacuna ventrale *mus.lac.v.* of a juliform millipede and the musculari apophyses sternales internus and externus *a.s.in.* and *a.s.ex.* of an oniscomorph in Part 4, text-figs. 3 and 8, pp. 308 and 354).

The rigidity of each separate endoskeletal unit of *Polyxenus* (formed by the fusion of a transverse tendon, a V-shaped bar, paired tracheal pouches and paired V-skeleton) must be strengthened by the tone of muscles *l* and *m* (text-fig. 2), whose contraction cannot cause movement. Contraction of the ventral longitudinal muscles *a.s.* (text-fig. 2) must pull successive endoskeletal units closer together, and the maintenance of even alignment of these units at any extension of the body must be effected by muscle *n* which obliquely links successive units, aided also by muscle *k* and the pleuro-sternals.

Defensive movements of each pleural spine rosette are mediated by muscles *u* and *w* operating on the pleurite from two segmental tendons (whose stability is maintained by the greater part of the skeleto-muscular system), and by the intrinsic muscles spanning the pleural lobe.

Since the arms of the Y-skeleton are united to the tracheal pouch, no independent movement of these structures is possible other than small movements allowed by bending of the skeletal bars, and since the tracheal pouches are united with the rest of the endoskeleton, no independent movements of the coxae are possible. The three muscles *d.s.c.*, *i* and *e* attached to the lateral, anterior and posterior edges of the bun-shaped coxae (text-figs. 2 and 3 A) must help to maintain the stability of the coxae rather than cause movement. The position of muscle *e*, arising from the tracheal pouch, suggests that this muscle is homologous with the retractor coxae of other millipedes, and muscle *i* appears to be a derivative of the protractor coxae which has shifted its origin from the tracheal pouch upwards to the transverse tendon. The positions of insertion of these two muscles on the coxae are moreover

comparable with those of a juliform millipede (cf. text-fig. 3 A and Part 6). The insertions on the anterior side of the coxae of muscle *i* and of the juliform protractor coxae lie farther from the middle line than do those of muscle *c* and the juliform retractor coxae on the posterior face of the coxa, and it will be shown in Part 6 that the limb musculature of the Juliformia is in most respects less specialized than that of other millipedes. Muscles *i* and *c* in *Polyxenus* might cause slight promotor and remotor oscillation of the coxa which could facilitate the large angle of swing of the leg, but the movement, if any, is too small to be detected by photography or by examination under a microscope. The primitive stepping function of muscles *i* and *c* has been suppressed and transferred to the unique promotor and remotor muscles of the pre-femur and femur.

The leg swings freely in all directions at the proximal and distal joints of the trochanter, and stepping is mainly caused by the pre-femoral and femoral muscles which pass through the passive trochanter (see Part 6). The very long remotor muscles not only pass from the Y-skeleton across to the other side of the body, but run to the following body segment and thereby utilize the other side of the same insertion as the promotor muscles, the inner ramus of the Y-skeleton. Fairly long remotor muscles are found in *Polydesmus* (Part 4, text-fig. 3 e and f, cf. the juliform millipede in text-fig. 3 c), but they are not as long as those of *Polyxenus*. The size of the remotor muscles of *Polyxenus* is presumably associated with the large angle of swing and powerful grip exerted by the legs. It is clear that in the absence of any ventral trunk exoskeleton precision of action by the leg is dependent upon the Y-skeleton on the coxa providing a rigid base. This rigidity is achieved by the evolution of elaborate yet thin bars of internal chitin and a complex of simple muscle strands such as exists in no other millipede. Complexity of musculature presumably evolved along with reduction in the exoskeleton, and originally simple muscle systems, such as the involvens complex and levatores apophyses anticae and posticae (see Part 4, text-fig. 3), have been sub-divided to form the elaborate dorso-sternals, tergo-sternals, pleuro-sternals and other muscles peculiar to *Polyxenus*. Many of these muscles serve their purpose by maintenance of tone, others also change in length with alterations in body extension, and some trunk muscles are concerned with effecting more extensive movements of some part or organ.

THE LIMBS, THE STRUCTURE OF THE CLAW AND THE METHOD OF ADHESION TO SMOOTH SURFACES.

The previously recognized peculiarities of the walking limbs of *Polyxenus* are the possession of the Y-skeleton, the ability to walk on the underside of a surface as smooth as glass, a capacity not found in any other millipede (O. von Rath, 1891; Verhoeff, 1896), and the apparent origin of the legs far from the middle line. The legs possess other specializations which can only be appreciated after a consideration of the mechanics of myriapodan leg movements (see Part 6).

The short trochanter, devoid of muscles, is inserted on the coxa nearer to the lateral margin than to the middle line. It is circular in section and serves as a 'universal joint', providing both the forward and backward swing normally effected by the joint between the coxa and the ring, and the levator and depressor movements in the transverse plane, as are usual between coxa and pre-femur (see Part 6). The legs are stout and their length relative to the ring volume is much as in the shorter-legged Juliformia and longer than in *Polyzonium* (see Part 4, Table II, column 4, p. 332, where the corresponding figure for *Polyxenus* is about 1.2*). The somewhat lateral insertion of the trochanter on the coxa allows the leg to flex up and down close to the body, remaining covered by the pleural spines at all times (Pl. 5, figs. 12 and 13, and Part 6), and the ventral surface of the body to be held very close to the ground.

The tarsal claw of *Polyxenus* is more complex than those of other Diplopoda. It has been figured more accurately by Silvestri (1903) than by subsequent workers, but structures which are clear in lactic acid mounts have previously been missed.

* It is difficult to estimate the ring volume of *Polyxenus* accurately.

The claw is composed of three parts united at the base. (1) A main claw, curved and blunt, possesses a secondary cusp which is posteriorly directed (*cl.* on text-figs. 4 *a* and *b*). Both cusps are almost fully sclerotized but with Azan the major cusp stains pale pink towards the tip. The main claw represents the 'paired short lappets' of Reinecke (1910). (2) From the anterior side of the claw base arises a thin flattened anterior process *a.p.* longer than the cusps, and ending in a very fine point. The process is fully sclerotized and so transparent as to be almost invisible in many media, and has therefore been missed by previous workers. It is easily seen in the living animal. Silvestri (1903) figures a comparable process on the claw of *Polyxenus patagonicus* and a similar process is present on the claws of *Juloidea* and *Nematophora* (see Part 6). (3) From the posterior and ventral side of the main claw projects a tongue-like adhesive lappet of thin cuticle, proximally staining red with Azan and distally being unstained and refractile. It curls round the claw, as indicated in text-fig. 4, its broad termination extending between the two cusps, beyond which it spreads out antero-posteriorly to the width of the claw base (*a.l.*, text-figs. 4 *a* and *c*). The integument of tarsus 2 is thicker dorsally than ventrally, and enlarges dorsally to form a cushion (text-fig. 4 *b*) as in other millipedes, serving as a fulcrum for articulation with the claw which is hinged at this point. The long apodeme (*a.c.*) leaves the claw ventrally and passes through four leg segments, showing a slight swelling near the claw. In other Diplopoda the apodeme of the claw extends only through the tarsus and just into the tibia (Part 6).

The main claw is rigid, and the anterior process is so thin that it bends freely. Eastham (1955) has shown that the rolling up of the butterfly proboscis is caused by the elasticity of a longitudinal rod of cuticle situated in the wall of the food groove on the galea, and this rod also stains red with Mallory. It may be suggested that the adhesive lappet acts as a suction disk by virtue of a similar elasticity. There are no independent effectors which move the lappet.

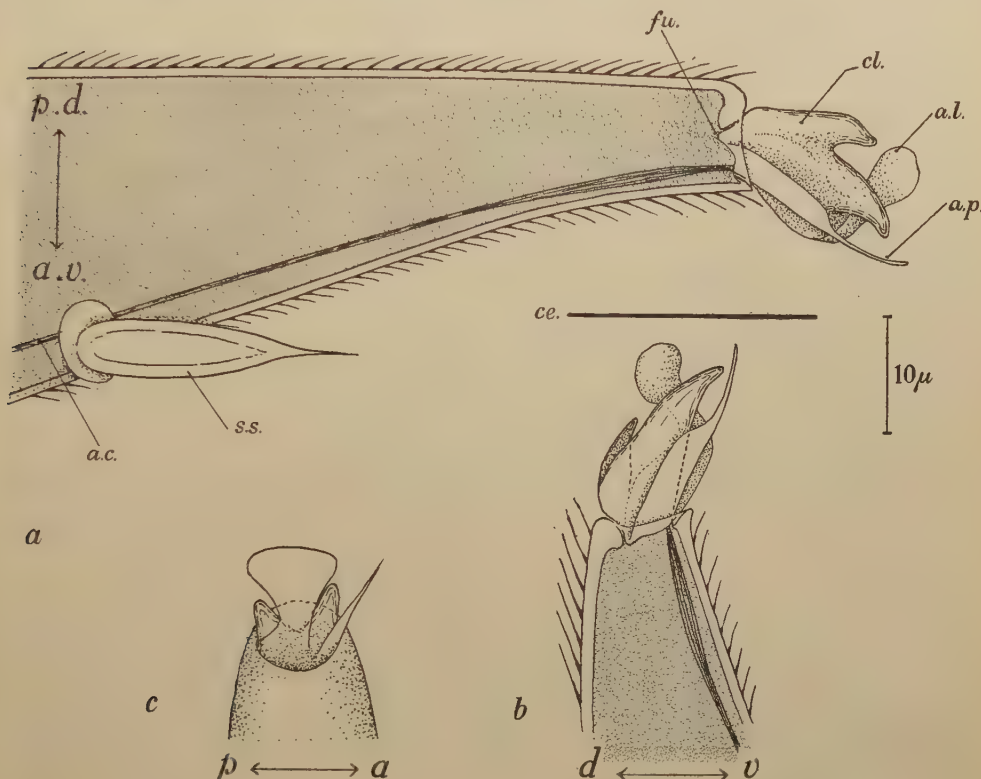
When the foot is put down the distal part of tarsus 2 is often held almost vertically to the substratum. Text-fig. 4 *b* shows the position of the limb tip just before it is put on the substratum, in this case a ceiling *ce.* The claws turn inwards towards the middle line, a position in which a maximum grip can be exerted on a rough surface, the leg tip being strongly flexed in a mesial direction. The large difference between the distances from the middle line of the limb tip when on and off the ground (Pl. 5, figs. 12 and 13) indicates the extent to which the leg is flexed mesially as it is put down. In ventral view *Glomeris* and *Polymicrodon* (Part 4, Pls. 53 and 54, figs. 17 and 28) show only a small difference in the distances of the leg tip from the body during the opposite phases of stepping. If the claws of *Polyxenus* find no grip, the adhesive lappet is automatically pressed down between the two cusps of the claw, as by a pitch fork, so that its terminal expansion is pressed on to the substratum on the morphologically dorsal side of the claw, and when so pressed down it adheres, presumably in the manner of a rubber suction disk. Text-fig. 4 *c* shows the fore-shortened appearance of the attached foot when viewed from above the coverglass on the underside of which the animal was walking. It is also probable that when the leg is promoted, the relative shortness of the posterior cusp on the claw results in both cusps being evenly pressed on to a flat surface, so causing an even pressure on the lappet at the moment of adhesion.

In order to bring tarsus 2 into a nearly vertical position, and to effect the observed stepping movements, great specializations of limb segments and of limb muscles have occurred, and no more specialized limbs have been found in the Diplopoda (see Part 6). The anterior process and adhesive lappet of *Polyxenus* show a convergent resemblance to the empodium, pulvilli and arolium of the insect foot.

LEG MOVEMENT, PACE DURATION AND SPEED.

The movements of the legs of *Polyxenus* differ conspicuously from those of other millipedes (see Part 4, text-fig. 5) in that leg 'n + 1' is put down close to the tip of

leg 'n' before the latter is raised, so resembling the stepping of the epimorphic Chilopoda. The left side of text-fig. 5 *a* shows the ranges of movement of the 13 legs, the heavy lines (superimposed) denoting the positions relative to the body of the limb tips during the propulsive backstroke, and the dotted line shows the limb tips during the middle of the recovery stroke. A slight fanning out of the fields of movement of the legs is seen antero-posteriorly, as occurs in some other Arthropoda without numerous legs (see Part 2, text-figs. 2 and 3).



TEXT-FIG. 4.

Tarsal claw of *Polyxenus*, (a) and (b) lactic acid mounts, (c) from a living specimen. The directions postero-dorsal, antero-ventral, dorsal, ventral, posterior and anterior are indicated by the lettered arrows.

- (a) Oblique anterior view of tarsus 2 and claw showing part of the dorsal aspect, exposing all parts of the claw, the main and posterior cusp *cl.*, the anterior process *a.p.* and the adhesive lappet *a.l.* The claw is hinged dorsally at the fulcrum *fu.* and the apodeme of the claw *a.c.* leaves the claw ventrally. The sensory spine *s.s.* lies on the anterior face of tarsus 2.
- (b) Anterior view of distal part of tarsus 2 and claw showing their positions just before adhesion to a ceiling *ce.* when the animal is running upside down. Tarsus 2 is sometimes held less vertically (see Part 6).
- (c) Appearance from above of the claw adhering by its lappet to the underside of a coverglass in the living animal, the microscope being focussed through the coverglass ceiling.

The coxa is almost or quite immovable, and the leg swings from the very mobile trochanter through a greater angle than that of any other millipede so far seen. In ventral view the legs of *Cylindroiulus* and *Glomeris* show apparent maximum angles of swing of 68° and 40° respectively while *Polyxenus* exceeds 80° (see Part 6).

Polyxenus can step more rapidly than any diplopod studied in Part 4. The shortest recorded pace duration by *Polyxenus* is about 0.2 sec. Only in the fleetest millipedes *Polymicrodon* and *Microchordeuma* was a pace duration as short as 0.2 sec. found, and the majority step more slowly (Part 4, p. 336).

The large angle of swing of the leg combined with more rapid stepping than in other millipedes suggests that fleetness is of significance to *Polyxenus*. A 4 mm. specimen can achieve at least 5 mm. per sec., while *Juliformia* with relatively longer legs, six times the body length or four times the body width, only show speeds of 8–13 mm. per sec.*

THE NUMBER OF METACHRONAL WAVES ALONG THE BODIES OF MYRIAPODA.

Arthropoda possessing numerous ambulatory legs can accommodate many metachronal waves of limb movement along the body at any one moment (see Part 3, Pl. 31, fig. 16; Pl. 35, fig. 40, and Part 4, Pl. 52, fig. 11 and Pl. 53, figs. 25–27), but the Myriapoda with the smaller numbers of pairs of ambulatory legs, *Cryptops* with 20, *Glomeris* with 17, *Lithobius* with 14, *Polyxenus* with 13 and *Pauropus* with 9, while naturally accommodating fewer waves, never show less than 2–2½ waves at any one moment when running freely (see Part 3, Pl. 32, figs. 20 and 26, text-fig. 6, p. 141; Part 4, Pl. 54, fig. 29 and the present Part, Pl. 5, figs. 12–16).

There is probably a mechanical reason for this similarity in animals so very different from one another. Instability may result from less than five or six supporting points distributed over the two sides of the body; only in *Pauropus* does the number occasionally drop to four or five when the fastest gait is employed (Part 3, text-fig. 12, p. 155), and the animal is then very unstable. Secondly, as the metachronal waves pass over the extremities, the smaller the total number of waves at any one moment, the longer does the momentarily unsupported anterior and posterior region become, and this must create ever varying strains on the musculature.

THE GAITS OF *POLYXENUS*.

The gaits which have been found in *Polyxenus* are shown in text-fig. 5 b–e, except for an anterior modification which is mentioned below. The range in pattern from (4.0 : 6.0) to (0.5 : 9.5) or slower is at first sight unexpected. A many-legged animal which appears to require speed might be expected to show a backstroke of relatively shorter duration than the forward stroke (cf. Chilopoda, Pauropoda and Diplopoda running fast). A relatively shorter backstroke is however impracticable for *Polyxenus* (see below).

The phase difference between successive legs in *Polyxenus* contrasts with that of all other Diplopoda, leg 'n + 1' being >0.5 of a pace in advance of leg n, so that successive propulsive legs converge, roughly as in the epimorphic Chilopoda, instead of diverging as in other Diplopoda (see Pl. 5, figs. 12–17; Part 3, text-fig. 1 a, p. 122, Pls. 31–33 and Part 4, text-fig. 5, p. 329, Pls. 52–55).

The employment of such a phase difference between successive legs is the obligatory result of the use of a large angle of swing. If it is advantageous to have not less than about 2½ metachronal waves along the body at one moment (see above), and there are 13 pairs of legs, the phase difference between successive legs must be either about 0.2 or 0.8.

Text-fig. 5 b–k shows the limb positions for the given gaits as they would appear in ventral view about the line 'ab' in text-fig. 5 a, if the phase difference between successive legs were uniform all along the body, and the same large angle of swing were used in all gaits. The distances between the legs are those found in the living animal (text-fig. 5 a) and the apparent lengths of the legs in the propulsive phase (heavy lines) and of the recovering legs (thin lines) are as shown in text-fig. 5 a, which is based on photographs in ventral view (see Pl. 5, figs. 12 and 13).

* Speed has been found to be roughly proportional to body length in millipedes of the same species.

Gait (4.0 : 6.0) with a phase difference between successive legs of 0.8 gives the disposition of the limbs shown in text-fig. 5*b*. This is a practicable gait, but if a phase difference of 0.2 were used (text-fig. 5*h*) a mechanically impossible disposition of the legs results, there being no available space for crossing of the legs (see Part 6). If the (4.0 : 6.0) gait were performed at a slightly smaller phase difference between successive legs (0.75 in text-fig. 5*i*), another impracticable disposition occurs with propulsive legs crossing each other (see Part 2, p. 111), and the degree of crossing would increase if the phase difference between successive legs were further reduced. Thus gait (4.0 : 6.0) can best be performed at a phase difference between successive legs of about 0.8 by an animal of the proportions of *Polyxenus* possessing only 13 pairs of legs which are moved through a large angle of swing. This gait is moreover the fastest that can be employed. Text-fig. 5*g* shows a faster (5.5 : 4.5) gait at a phase difference between successive legs of 0.8; it is impracticable for the same reasons indicating that the gait in text-fig. 5*i* is impracticable. A (5.5 : 4.5) gait needs a phase difference of 0.85 (text-fig. 5*f*) to eliminate crossing of propulsive legs by *Polyxenus*. This gait however has not been found, presumably because the groups of propulsive legs are too far apart (see above), and possibly there may be too few adhesive legs at any one moment for upside-down running.

The slower gaits shown in text-fig. 5*c-e* similarly have obligatory phase differences between successive legs, gaits (3.0 : 7.0) (2.0 : 8.0) and (0.5 : 9.5) needing phase differences of about 0.75, 0.65 and 0.6 respectively. Phase differences of 0.25, 0.35 and 0.4 respectively, giving the type of disposition of propulsive legs found in other Diplopoda, result in undesirable crossing, as in text-fig. 5*j*; slightly smaller phase differences in each case lead to crossing of the propulsive legs such as is seen in text-fig. 5*g* and *i*, and larger phase differences in each case needlessly separate the groups of propulsive legs and consequently the length of the momentarily unsupported extremities of the body (see the different distances between the groups of propulsive legs in text-fig. 5*f* and *g*).

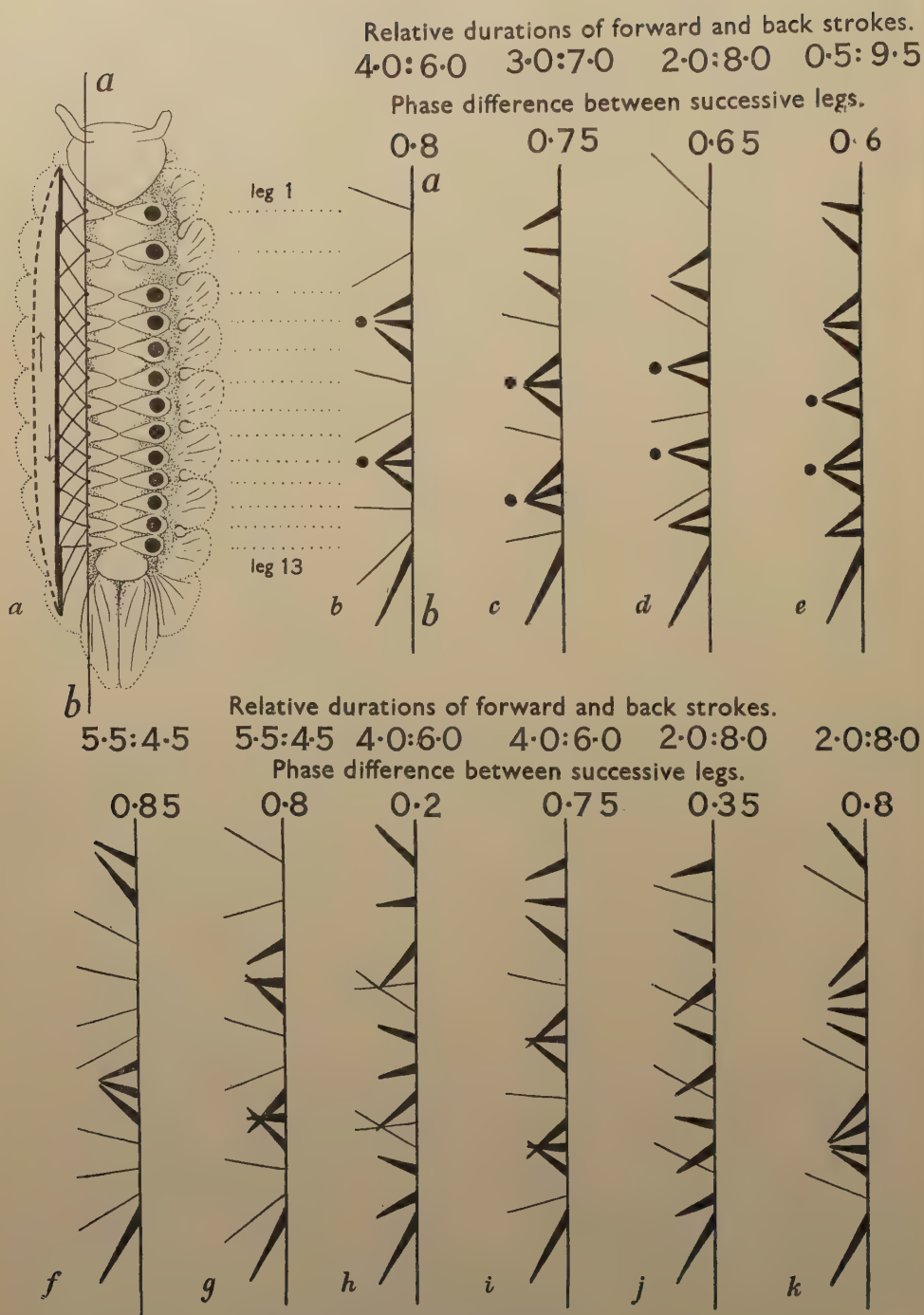
It will be noted that the greater distance between the origins of the anterior legs, where there is only one pair per ring, results in their tips being less close together in the propulsive phase than are those of the more posterior legs. This is seen most clearly in the moments shown by text-fig. 5*c, g* and *i*. It is much less marked in Pl. 5, figs. 14 and 16 because the animal is making adjustments in anterior phase differences which tend to eliminate this effect. Comparisons between the actual performance of *Polyxenus* on experimental runs with mathematical representations of the various gaits show that an even phase difference between successive legs usually is not maintained all along the body, the phase differences between the anterior three legs being less than it is further back, a feature doubtless correlated with the positions of origin of the anterior legs.

The photographs on Pl. 5, figs. 14, 15 and 16 correspond, except anteriorly, with the gaits shown in text-fig. 5*d, c* and *b* respectively. The slower gait (0.5 : 9.5) in text-fig. 5*e* is represented here by the track shown on text-fig. 6*a* (see below). Other leg dispositions such as that in text-fig. 5*k* are found when the animal is changing its speed, in this case slowing down from gait (4.0 : 6.0) with the phase difference not yet reduced. It is probable that smaller angles of swing of the leg are used at the slower speeds. Small changes in the angle of swing of legs are usually not easy to record (see Part 2, p. 105 and Table 1 and Part 4, p. 334).

Polyxenus runs upside down and 'right way up' with equal readiness on any surface however smooth, and the gaits employed are similar in the two situations (cf. fig. 17 with figs. 15 and 16, Pl. 5).

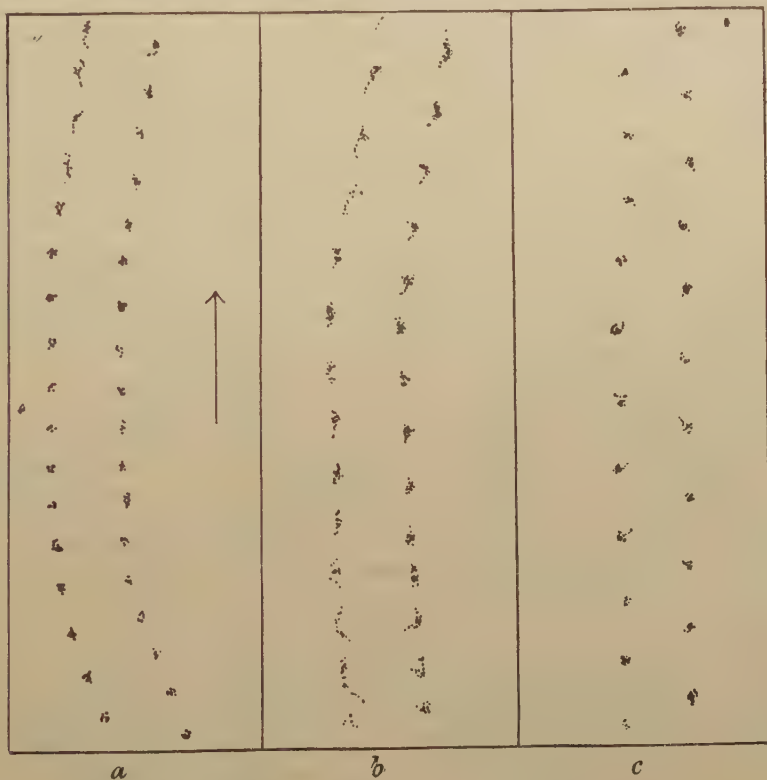
THE PHASE RELATIONSHIP BETWEEN THE PAIRED LEGS.

The stride lengths of the several gaits shown in text-fig. 5*b-e* are 1.0, 0.75, 0.5 and 0.45 mm. respectively for a 4 mm. *Polyxenus*, the distances between the black dots. In spite of small size, the suckered feet of *Polyxenus* leave clear tracks



TEXT-FIG. 5, (For description see p. 173).

when walking on smoked paper. Text-fig. 6 *c* shows the track of a 4 mm. animal moving at 2.5 mm. per sec. by gait (3.0 : 7.0) giving strides of 0.7 mm. Approximately common footprints are formed by all the legs of one side, indicating that the phase difference between the anterior legs was less than that between the posterior legs (see above). These common footprints of the two sides of the body exactly alternate, indicating that the phase difference between the paired legs was 0.5. Text-fig. 6 *a* shows the track of gait (0.5 : 9.5) giving strides of 0.45 mm. and a speed of 0.85 mm. The common footprints of the two sides are here level, indicating that the animal used the paired legs in the same phase. Text-fig. 6 *b* shows an



TEXT-FIG. 6.

Tracks left by a 4 mm. *Polyxenus* walking on smoked paper, the tracks being photographed and printed in reverse. (a) animal moving at 0.85 mm. per sec. by gait (0.5 : 9.5), p.d. 0.6 (see text-fig. 5 *e*), giving strides of 0.45 mm.; paired legs in similar phase; (b) animal moving at 1.2 mm. per sec. by gait (2.0 : 8.0), p.d. 0.65 (see text-fig. 5 *d*), giving strides of 0.5 mm.; phase difference between paired legs on the lower part of the record 0 and on the upper part 0.25–0.3; (c) animal moving at 2.5 mm. per sec. by gait (3.0 : 7.0); p.d. 0.75 (see text-fig. 5 *c*), giving strides of 0.7 mm., phase difference between paired legs 0.5.

TEXT-FIG. 5.

The gaits of *Polyxenus lagurus*.

(a) Diagram scaled upon photographs of the living animals in ventral view when walking at maximum body length. The coxae approximating towards the middle line are shown in white: the legs on the right are cut off at the trochanter (black); and on the left the range of movement of each leg is shown (see text), the heavy line denoting the position of the limb tips during the propulsive backstroke and the interrupted line showing the approximate position of the limb tips during the recovery forward stroke. Figures (b–k) show the calculated positions of the legs in ventral view when performing the given gaits, based upon the line *ab* in fig. *a*, and using the leg lengths in propulsive and recovery strokes as seen in ventral view. Only the gaits of figs. b–e and k are practicable (see text).

intermediate type of track, made by gait (2.0 : 8.0) giving strides of 0.52 mm. and a speed of 1.2 mm. The footprints in each set are more scattered; in the lower part of the record the paired legs moved in the same phase, while in the upper part their phase difference was 0.25–0.3 (cf. tracks of epimorphic Chilopoda in Part 3, text-figs. 4 and 5).

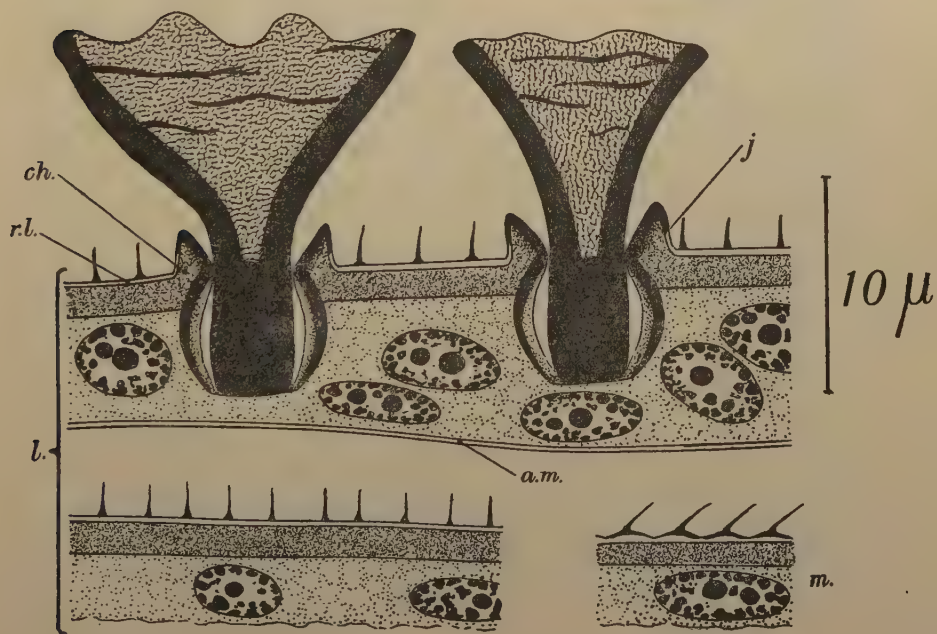
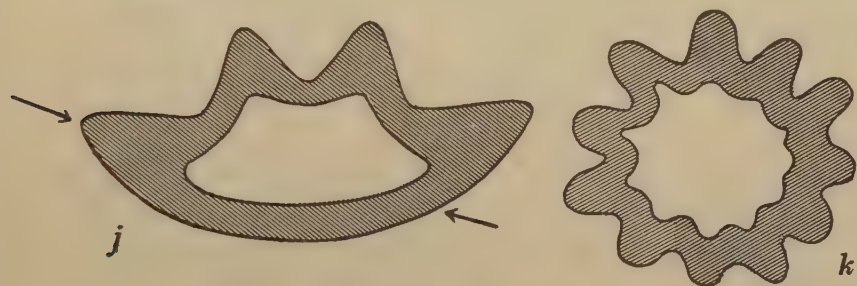
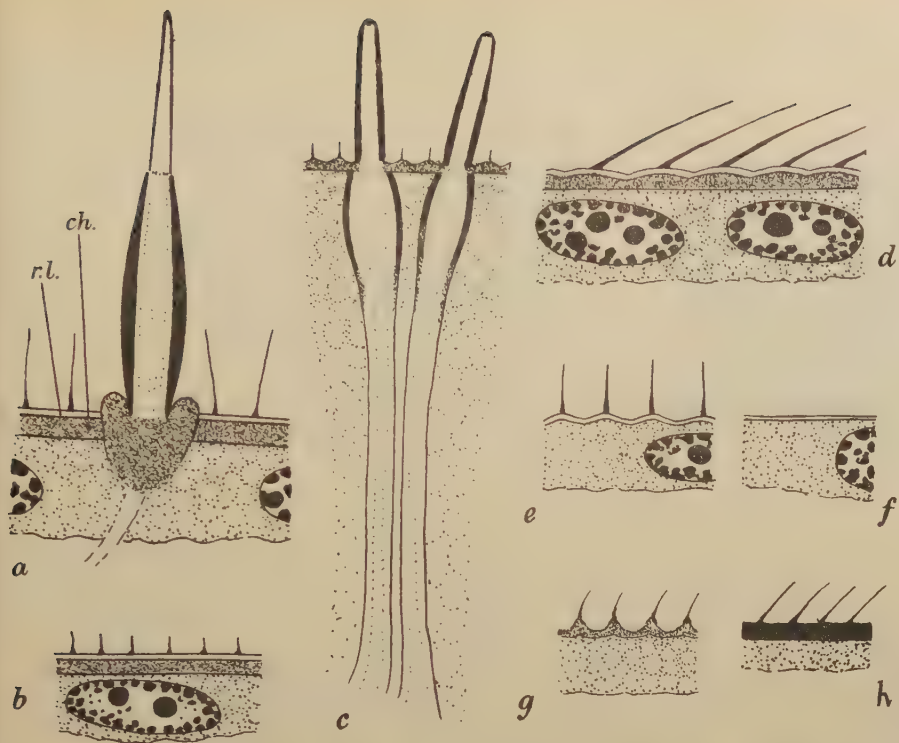
In Pl. 5, figs. 12 and 13 the same gait (4.0 : 6.0) is seen in ventral view; the paired legs are in similar phase in fig. 12 but show a difference of 0.3 in fig. 13. It is probable that the records of the tracks, which show uniformity over considerable distances, indicate a more usual pattern of locomotory movements than do the photographs taken from below. The animals walked freely in the former conditions but were subjected to continual interference in the latter. Thus in the faster gaits (3.0 : 7.0) and (4.0 : 6.0) the paired legs usually move in opposite phase, in the slow gait (0.5 : 9.5) and in slower ones they move in the same phase, and intermediate phase differences between the paired legs are found in the intermediate gaits.

In Part 2, p. 110 a summary was given of the conditions which are associated with the use of paired legs in similar or in opposite phase. Myriapods whose most significant habit requires a fast gait, with the backstroke of relatively shorter duration than the forward stroke, use the paired legs in opposite phase (Chilopoda and Pauropoda, see Part 3), while those in which the most significant habit requires a gait with the backstroke of relatively longer duration than the forward stroke use the paired legs in similar phase (Diplopoda, see Part 4). *Polyxenus* attempts speed, but for mechanical reasons cannot employ a gait with a backstroke of shorter duration than the forward stroke. The use of an opposite phase relationship of the paired legs in the faster gaits in *Polyxenus* which are of the 'bottom gear' pattern appears to be due to the convergence of the propulsive legs which results in the body being supported by widely separated points, as in the epimorphic Chilopoda and Pauropoda (see Part 3, text-figs. 3 and 12, pp. 125 and 155). When these points on one side of the body are farthest apart, as in gait (4.0 : 6.0), most adequate support is obtained when these points alternate on the two sides, but when most of the legs are in the propulsive phase at one moment (as in gait (0.5 : 9.5), text-fig. 5 e), more even pushing will result if the paired legs are moved in the same phase.

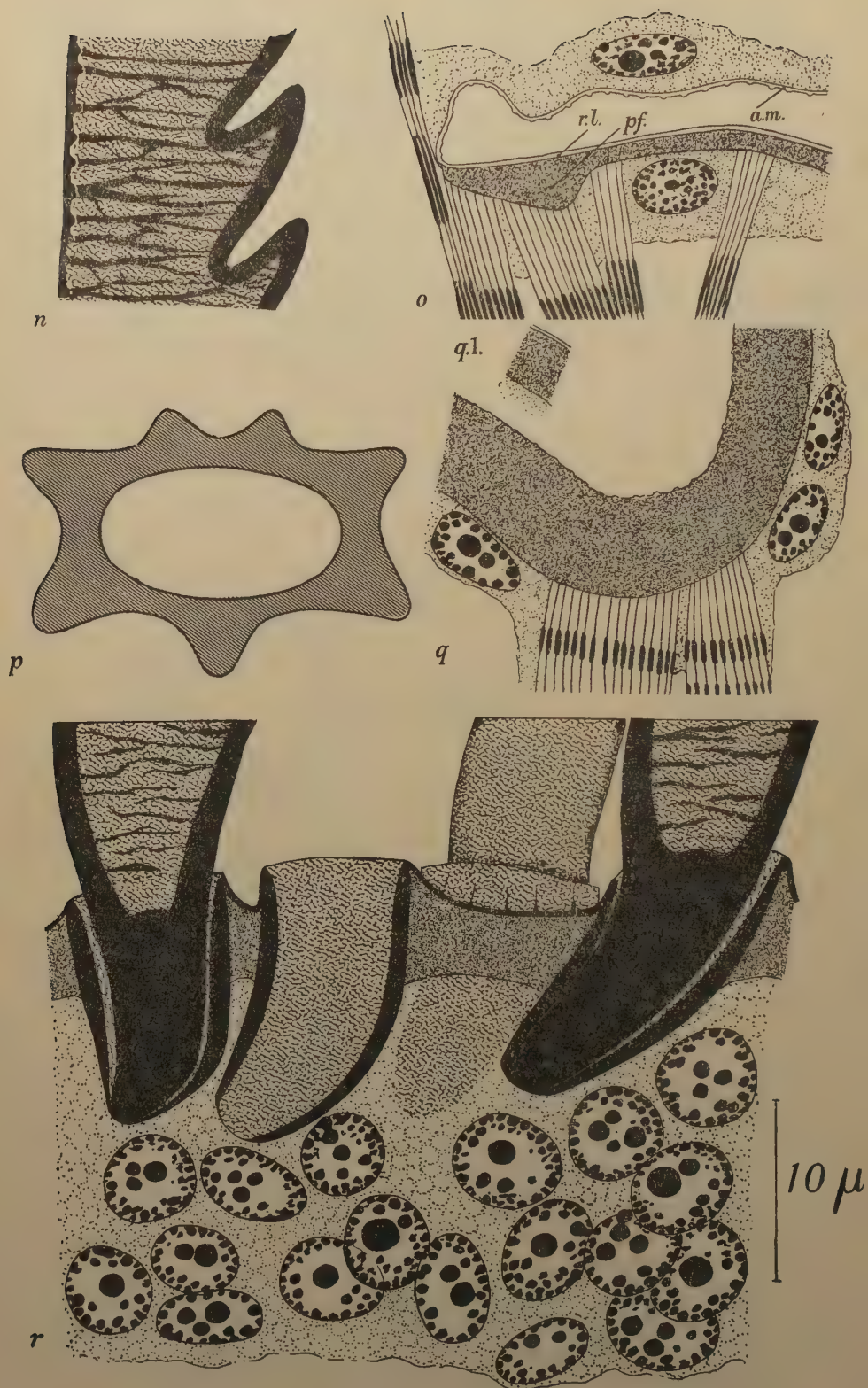
Only rarely does a species use phase differences between the paired legs of both more than and less than 0.5, see *Peripatus* (Part 1) and the geophilomorph centipedes (Part 3). This feature may be primitive in *Peripatus*, but it is absent in Diplopoda other than *Pselaphognatha*, and since *Polyxenus* appears to have had diplopod ancestors (see below), the great range of phase relationship shown by this animal is probably secondary.

THE CUTICLE (in collaboration with J. G. Blower).

The cuticle of *Polyxenus* differs from that of all other Diplopoda in the absence of calcification, and the whole is flexible to varying degrees in different parts. A rigid integument is necessary for a pushing habit (see Part 4, pp. 303 and 352), and since *Polyxenus* does not burrow by pushing, and on the contrary excels at walking on smooth ceilings, the lightest possible integument is the more appropriate. The cuticle of *Polyxenus* is very thin, about 0.7–1.8 μ . Those of *Blaniulus* and *Schizophylum* are about 13 μ and 50 μ thick respectively, while those of the abdominal tergites of *Periplaneta* and of *Polydesmus* are about 35 μ thick. The flexible cuticle of a *Peripatus* ten times the length of *Polyxenus* is less than 1 μ thick, and with Mallory or Azan it shows a non-staining surface refractile layer covering an elaborate red layer and below that a blue zone. The refractile layer is easily seen forming the edge of the small crest over each ectodermal cell (Manton, 1937, Pl. 39). These features are normal in the much thicker scutes of other Arthropoda, although the red staining layer usually lacks external ridges. *Polyxenus* however scarcely shows the triple-layered staining reactions, and over much of the body the entire cuticle takes either the red or blue of Azan and of Mallory. The structure of the integument



TEXT-FIG. 7. (For description see p. 177).



TEXT-FIG. 8. (For description see p. 177).

in the various regions is described below in terms of its reactions to this Azan stain combination, which are very similar to those with Mallory.

Most of the body surface is covered by non-staining refractile cuticle and the greater part of the partially sclerotized red-staining cuticle present on the body is located in the complex spines and in the minute spinules which clothe all exposed surfaces. The U, V and Y-shaped skeletal bars and the prophragma bar all stain dark blue, but the unmodified chitin covering the body, if it stains blue, appears a paler blue except at the joints between the leg segments, where apart from the arthrodial membrane the blue is more intense, as it is at the posterior insertion of the paratergalis muscle.

The thickest and *structurally most simple patch of cuticle* forms the point of insertion of the paratergalis muscle between pleurite and tergite (text-figs. 2 and 3 *a, f, s, g.* and *q*). A refractile surface layer is either absent or very thin over the middle of this patch, and the cuticle here can be pulled into a concave form by the tension of the large muscle. The refractile layer becomes apparent peripherally (text-fig. 8*q* 1) and continues over the whole dorsal and lateral surfaces.

The *tergite* and *pleurite* are essentially similar in structure (text-figs. 7*l* and 7*b*). A blue staining layer *ch.* a little over $1\ \mu$ in thickness is covered by a thin refractile layer *r.l.* and the whole surface bears spinules at intervals of about $1.4\ \mu$. The blue layer becomes thickened to form the rim at the anterior margin of the tergite and the spinules disappear from the refractile layer near the inter-ring junction (text-fig. 8*o*). Ventro-laterally the pleurite is a little thinner than the tergite and the spinules are shorter (text-fig. 7*b*). Antero-laterally on the tergite the red colour spreads from the spinule bases into the surface of the refractile zone, giving an irregular outer red covering (text-fig. 7*m*).

Near the large tergal and pleural spines the ectoderm is thicker than elsewhere, and into it sink the sockets which carry the shanks of these spines (text-fig. 7*l* upper part, and 8*r*). The vase-shaped sockets stain red with Azan but appear more refractile and less coloured with Mallory, in unstained preparations they are amber coloured (i.e. strongly sclerotized). The neck of the 'vase' grips the solid shank of the spine, which arises from the base of the socket, and the rim of the vase folds back to join the surface refractile layer and loses its red colour, as shown in text-fig. 7*l* at *j*. On the pleurite where the spines are larger, the sockets are larger and closer

TEXT-FIGS. 7 and 8.

Sections through the ectoderm and overlying cuticle and spines in the positions shown by the marked rings in text-figs. 1-3. Unmodified chitin (blue with Azan) *ch.* shown by mechanical tint, partly sclerotized chitin (red with Azan) black; completely sclerotized chitin (non-staining refractile) *r.l.* white; *a.m.* arthrodial membrane between tergites; *p.f.* thickened rim on anterior margin of tergite functioning as a prophragma.

- (*a*) Through prefemur cuticle and sensory seta (see fig. 3 *A, f. 7.a.*); (*b*) through pleural lobe just below origin of spine rosette (see fig. 3 *A, f. 7.b.*); (*c*) through sense setae on gnathochilarium; (*d*) through distal part of femur (see fig. 3 *A, f. 7.d.*); (*e*) through exposed part of lateral body wall (see fig. 1, *f. 7.e.*); (*f*) through lateral body wall where it can fold against the ring in front or against the coxa (see figs. 2 and 3 *A, f. 7.f.*); (*g*) through sternal region, both triangles and furrows (see fig. 1, *f. 7.g.*); (*h*) through tarsus 2 near claw (see fig. 3 *A, f. 7.h.*); (*j*) T.S. of tergal spine, details of wall structure omitted; (*k*) T.S. of pleural spine, details of wall structure omitted; (*l*) T.S. where two tergites overlap at the level of a tergal spine row, the insertions of two tergal spines are cut longitudinally, the bases of the spines being shown, thin arthrodial membrane covers the underside of the outer tergite (see fig. 2, *f. 7.l.*); (*m*) through antero-lateral part of tergite near the 'prophragma' (see fig. 2, *f. 7.m.*); (*n*) L.S. of part of pleurite spine to show structure (see text); (*o*) frontal section through anterior edge of tergite and arthrodial membrane (see fig. 2, *f. 8.o.*); (*p*) T.S. through pleurite spine, details of wall structure omitted; (*q*) through middle of thick flexible cuticle between tergite and pleurite on to which flexor paratergalis muscle is attached (see fig. 2, *f. 8.q.*) (*q* 1) through edge of same; (*r*) through pleurite and insertions of pleural spines (see fig. 2, *f. 8.r.*).

together, and the surface of the cuticle between the spine sockets is concave (text-fig. 8 *r*). The outer layer of the cuticle between the sockets stains red and bears the usual spinules while the inner layer stains blue and is thicker than on the tergite. The surface zone uniting the spine sockets is clearly the same morphological structure on tergite and pleurite, although the staining reactions indicate a different degree of sclerotization in the two locations.

The general form of the *large spines* has been figured by Silvestri (1903), Reinecke (1910) and others. Verhoeff (1928) noted that the spines are air filled. The large internal cavity (text-figs. 7 *j*, *k* and 8 *p*) extends almost to the base of the spine (text-figs. 7 *l* and 8 *r* and Pl. 5, figs. 18 and 19). The whole spine stains bright red, and when unstained is refractile and amber coloured (i.e. sclerotized), and the utmost economy in material is apparent. Where spines are exposed on all sides, longitudinal rows of teeth are similarly situated, but when one side lies against the body, as on the tergal spines, no teeth are found on that face (see text-fig. 7 *j* and Pl. 5, fig. 19). The wall of the spine is thick where it is evaginated to form teeth (see right side of text-fig. 8 *n*), but in between the rows of teeth the wall is thin, as shown on the left side of the figure. The outer surface of the spine is smooth, but the inner surface is raised into irregular transverse ridges (text-fig. 8 *n*) which, with the tooth rows, must give rigidity to the otherwise thin-walled but very large spine, and the spines must be light.

The *flexible parts of the body wall* situated between the legs and the scutes are covered by very thin cuticle which may appear entirely refractile, as on the lower side of the pleural lobes (text-fig. 7 *e*) or it may stain blue (text-fig. 7 *g*) as on the pedigerous lamina. In both the integument humps up towards each spinule, and more markedly where the chitin is unmodified (blue). Laterally where the body wall folds near successive legs, and on the arthrodial membranes, a thin flat refractile layer only is present (text-fig. 7 *f*). Spinules are lacking, but there are small surface humps where an arthrodial membrane may become concave (text-figs. 7 *l* and 8 *o*, *a.m.*). The cuticle states shown in text-fig. 7 *e*, *f* and *g* must be homologous, but they differ locally in their degree of sclerotization, as was noted above for the scute structure.

The *cuticle of the proximal leg segments* is essentially like that of the scutes, but the blue layer is thinner, the spinules are longer and the refractile surface zone may stain slightly pink over the coxa and elsewhere (text-fig. 7 *a* and *d*). Parts of the leg show a spreading of the red colour from the bases of the spinules, much as in text-fig. 7 *m*, and towards the claw the cuticle of tarsus 2 becomes entirely red with the spinules set closer together (text-fig. 7 *h*).

The cuticle of *Polyxenus* exhibits a basic similarity to that of other Diplopoda in spite of its thin and flexible nature and lack of calcification. Blower (1951) has shown that the diplopod sclerite is chitinous throughout. With Mallory stain it shows an outer non-staining refractile zone of fully sclerotized material; below this is a thin zone of partly sclerotized material staining red and the bulk of the cuticle is formed by the various endocuticular layers of blue-staining unmodified chitin (see Blower, 1951, text-fig. 5). The sclerites of Chilopoda, Crustacea and Insecta contrast in showing a greater thickness of red staining and/or refractile material. Rigidity of the integument in Diplopoda is attained largely by calcification of the outer endocuticle, while the lesser rigidity of the sclerites of Chilopoda results from more extensive sclerotization and less calcification.

A large number of layers within the cuticle of Arthropoda have been recognized by various workers and these zones are difficult to homologize from one group to another. Dennell & Malek (1954, 1955), Blower (1950, 1951) and others have

shown the progressive nature of the phenomena leading to sclerotization. A conception of a basically layered cuticle possesses limitations because 'layers' resulting from different degrees of sclerotization or of impregnation by pro-sclerotin have no fundamental reality. The view "that the myriapod cuticle might be considered as a chitinous matrix impregnated to varying extents by pro-sclerotin which may or may not be tanned" (Blower, 1951) is supported by the variety of local states of the cuticle in *Polyxenus*. It can scarcely be doubted that the cuticles shown in text-fig. 7 *e*, *f*, *g* and *h* are morphologically homologous. It would be difficult to explain their differences on a basis of the presence or absence of various layers; but the appearances of these figures, and of all intermediates, are readily understandable on a conception of progressive modification of a single basic layer, unmodified chitin, blue in fig. *g*, partly sclerotized chitin, red in fig. *h*, and fully sclerotized chitin, refractile in figs. *e* and *f*. The cuticle of these regions is entirely modified into one of these various states, so that no layers result. Similarly the difference between text-fig. 7 *a*, *b*, *d* and *l* where the surface zone is non-staining, and text-figs. 7 *m* and 8 *r* where the surface zone is red, indicates a lesser degree of sclerotization of the same basic structure in the latter than in the former, although there are difficulties in seeing the 'red' in thin, highly diffracting, surface membranes.

The local differences in the structure of the cuticle described above most probably reflect varying mechanical properties associated with different skeletal functions. In addition, the cuticle is strongly water repellent, which, as has been suggested, is no doubt a defensive adaptation to the possibility of temporary flooding of the small spaces frequented by *Polyxenus*. The distribution of cuticular lipid is important in this respect and has been revealed by sudan black treatment of frozen sections of formol/calcium fixed material.

As in other diplopods (Blower, 1952) there is evidence of surface accumulations of lipid which appear to originate from the epidermis by way of very fine ducts which pass through the cuticle. Some of the ducts contain lipid and originate from small accumulations of lipid at their bases. Variation in the appearance of these glandular regions of the epidermis suggest an asynchronous secretion of lipid throughout the instar.

Lipid is also an essential constituent of prosclerotin and remains demonstrable by sudan black in regions where sclerotization is not extensive or is incomplete (Blower, 1952; Dennell & Malek, 1955). It has also been shown (op. cit.) that staining with the red of Mallory's combination goes hand in hand with sudan colouring. In *Polyxenus* there is a similar correspondence of sudan colouring and red staining with Azan. Thus all the red staining regions as described above take sudan. This sudan colouring is most evident in the large spines, especially at their bases and in the walls of their socket-like insertions.

It is not clear just how far this 'structural lipid' may contribute to the hydrofuge property of the cuticle, nor is it always possible, in such a thin membrane, to distinguish the 'structural' from the surface lipid which may secondarily impregnate the outer layers of the cuticle. However, the presence of lipid-filled ducts passing through to the surface strongly supports the impression of a surface layer of free lipid. It does not seem possible that surface irregularities (spines, spinules, etc.) could, by themselves, account for the water repellence of the surface but, on the other hand, if they are all covered with a water-repellent lipid they will trap an extensive layer of air at the surface which may have a respiratory significance.

THE EVOLUTION AND AFFINITIES OF THE PSELAPHOGNATHA.

The details recorded above indicate that both the locomotory mechanism and the morphology of *Polyxenus* are in no way primitive. Their peculiarities are understandable on two assumptions. Firstly, that the ancestors of the Pselaphognatha were Diplopoda in which the habits of pushing into the substratum and of rolling up were of significance, and that diplo-segments, the suppression of one pair

of legs on rings 2-4, etc. were evolved in association with these habits (see Part 4, pp. 325 and 349). Secondly, that pushing and rolling up were later abandoned as the animals became secondarily adapted to living in very narrow crevices and to running on the ceiling of their hides (see also p. 183). New provisions against predators and water were acquired, together with great leg specialization (see Part 6) and a speedier method of walking about. Proficiency in living on the ceiling of a crevice makes the capacity to roll up superfluous, as it could not be practised, and the evolution of the *Polyxenus* type of protection by large spines is incompatible with rolling up.

Shuleikin (1937) and Zenkevich (1945) have drawn attention to the way in which different types of locomotory organs supply an animal with maximum speeds of movement only within certain size ranges. Fish less than 1 cm. in length no longer swim faster than copepods, and copepods below 0.01 cm. in length are less fast moving than ciliary swimmers. Different sorts of locomotory organs are appropriate for different sized animals if maximum speeds are to be achieved. This general principle doubtless applies to other functions besides the attainment of fast locomotion. It was shown in Part 4 how size affects the pushing power of millipedes and, as noted above (p. 153), *Polyxenus* may be below a minimal size for effective burrowing in the diplopod manner. Small size may have been the circumstance most closely connected with a supposed change in habit by the diplopod ancestors of the Pselaphognatha. Taking refuge in rocky cracks would be an easy habit to adopt if small size rendered the original pushing habit less effective (see Part 4, p. 343), or conversely small size might have a selective value to diplopods escaping predators by entering narrow places (see further p. 184).

MORPHOLOGICAL SPECIALIZATIONS CONNECTED WITH THE PRESENT HABITS.

Specializations of Polyxenus for protection and for entering narrow places include :

(1) the extremely hydrofuge cuticle with numerous spinules and air-filled spines ; (2) the flattened body ; (3) the mobile posterior spine bundles and mobile pleural lobes bearing spine rosettes, and (4) the extensive areas of flexible cuticle which facilitate this mobility ; (5) the capacity to telescope the body when stationary, made possible by the elaborate folding of the pedigerous lamina, the form of the inter-ring joint, and the muscles to the inter-ring arthrodial membrane and folds of the pedigerous lamina, which have not been seen in any other millipede. Protection by spines replaces the normal diplopod protection by a hard cuticle and stink glands. Restriction of the rigid parts of the ring renders defence by spines more efficient than it would be if the rings did not telescope. Stink glands, if they were present ancestrally, might be of limited service to an animal which keeps its enemies 'at arm's length', and the manner of discharge of the glands employed by the Juliformia (see Part 4, p. 328) could scarcely be combined with such a telescopic body.

The extensibility of the body, the transverse folding of the cuticle, and its flexibility are reminiscent of the conditions in *Peripatus*, but the 'soft body' of the Onychophora is probably primitive (Part 3, p. 160). The more numerous transverse furrows of *Peripatus* are easily formed because the sensory spine-bearing papillae are roughly arranged in rows and folding occurs between the rows. There are no special muscles controlling the folds. The flexible cuticle of *Polyxenus* is entirely unlike that of *Peripatus*, and is clearly derivable from the type of cuticle found in other Diplopoda : the complex muscle penicilli of *Polyxenus* also could have been evolved from a basically diplopodan musculature (see pp. 161 and 167), and this is quite unlike the simple sheets of circular, oblique and longitudinal muscles of the Onychophora. The 'soft body' of the Pselaphognatha therefore appears to be a specialization and not a primitive feature.

(6) The presence of trichobothria on the head of *Polyxenus* but on no other Diplopoda may be related to the habits, although little is known of the function of these organs. Trichobothria on the antero-lateral parts of the head are incompatible with

the diplopod method of pushing, and were presumably absent in the diplopodan ancestors of the *Pselaphognatha*. Trichobothria are found in Symphyla and Pauropoda, both groups comprising animals living in crevices of a different kind. The presence of these organs in the *Pselaphognatha*, Symphyla and Pauropoda appears to be an example of independent evolution of a similar sense organ, just as compound eyes have been evolved independently by some Crustacea and Insecta.

Specializations of Polyxenus which enable it to live on smooth ceilings, and thus to inhabit a niche where predators cannot easily follow, involve the whole organization of the trunk region. Extreme lightness has been achieved by: (7) absence of calcification of the cuticle; (8) by the very light yet strong construction of the large protective spines; and (9) by reduction of the skeletal units to a minimum; the unique lattice formed by U, V and Y-shaped skeletal rods and tracheal pouches presumably was evolved from a normal diplopodan endoskeleton.

The ability to run on smooth surfaces at any angle has involved the utmost specialization of limbs and skeleto-muscular systems. These specializations include: (10) all the details of the trunk skeleto-muscular systems described above which maintain the stability of the Y-skeleton; (11) the staggering of the dorsal and ventral elements; (12) the form and immobility of the coxa; (13) the unique promotor and remotor leg muscles operating from the pre-femur and femur; (14) the form and situation of the trochanter; (15) the extra tarsal segment (see Part 6); (16) the very long apodeme of the claw; (17) the whole limb musculature (see Part 6); and (18) the adhesive lappet on the claw.

The basic form of the leg and its muscles in *Polyxenus* and *Lophoproctus* are similar. The legs of *Lophoproctus* are relatively longer and more slender, and may be expected to exert as powerful a grip (see Part 6), but the claw lacks an adhesive lappet. This structure in *Polyxenus* appears to represent a final refinement conferring the ability to walk upside down on very smooth surfaces, and not to be a feature upon which the whole evolution of the *Pselaphognatha* has depended. If the adhesive lappet was evolved by gradual outgrowth from the claw, its short initial stages would give adhesion from the ventral side of the claw, and during the backstroke the distal part of the leg would be held much as in the *Juliformia* and not so vertically as in *Polyxenus*, and the grip by the claws would be less clinging since the tips of a pair would not converge. Gradual elongation of the adhesive lappet would allow the employment of a more vertical position of the tarsus, and this has entailed the formation of an extra tarsal joint (see Part 6).

The bun-shaped immobile coxa appears to represent a unique method of obtaining a more lateral origin of the movable part of the leg, which makes possible the use of a large angle of swing yet keeps the ventral body surface very close to the substratum, and thus protection by the pleural spine rosettes is effective. The *Polydesmoidea* achieve a more lateral origin of the legs than is found in other Diplopoda, but by means of transverse bulges on the pedigerous lamina (see Part 4, p. 314), and the lateral limb origin in *Polyxenus* also results in the ventral body surface at times being held very close to the ground. An insertion of the legs near the mid-ventral line is needed by Diplopoda which burrow by head-on pushing (Part 4, p. 342) and this feature was probably present in the pushing ancestors of the *Pselaphognatha* in common with other groups, since the immovable coxae of the *Pselaphognatha* closely approximate to the middle line.

LOCOMOTORY SPECIALIZATIONS.

The gaits employed and the speeds achieved by *Polyxenus* are also indicative of great specialization. *Polyxenus* has achieved some measure of fleetness by the use of a short leg, a large angle of swing of the leg, a slightly quicker pace than is usual in Diplopoda and a 'bottom gear' gait. This method of obtaining speed is unique among the major groups of the many-legged Arthropoda so far examined (for Myriapoda, see Part 2, Tables 1 and 2, pp. 104-5). Short legs are necessary for the habits

of *Polyxenus* : longer legs would be unsuitable for crevices and would be exposed. The large angle of swing of the leg has made gaits faster than (4.0 : 6.0) impracticable for a series of legs so close together, a closeness resulting from the inheritance of diplo-segments. In contrast, gait (7.5 : 2.5) by the Scolopendromorpha and gait (6.6 : 3.3) by the Spirostreptomorpha may be found in fast running. The legs in both these groups are longer than in *Polyxenus*, and the angle of swing of the leg in most Diplopoda is less. The Scolopendromorpha can use a fast gait with large angles of swing by short legs (compare Part 3, Pl. 33, fig. 30 with Pl. 5, figs. 13-16 of the present Part), because the distance between one leg and the next relative to the leg length is greater than it is in *Polyxenus*. The apparent lateral origin of the legs in *Polyxenus* gives greater scope for wide movements and superficially approaches the scolopendromorph condition, as well as allowing *Polyxenus* to enter the narrowest places (see Part 6).

Polyxenus does not show a primitive diplopodan locomotory mechanism, but on the contrary a very specialized one, made possible by the many structural specializations. The gaits of *Polyxenus* are derivable from those which are usual in the Diplopoda, although the differences are very conspicuous. It has been shown above how mechanical factors necessitate the adoption of a much larger phase difference between successive legs than occurs in other Diplopoda, and a variable phase difference between the paired legs. These resemblances to the Chilopoda in gait and in limb origin are but partial, and have clearly been independently evolved, and the pace duration, although shorter than in most Diplopoda, is closer to the durations found in this group than it is to the quickly stepping Chilopoda where the pace duration may be but one-fifth of that shown by *Polyxenus*.

In this series of studies on arthropod locomotion no reference has been made to the neurological aspect of the problem, important though this is. It may be noted that a postulated change in habits from those of ancestral Diplopoda to present-day Pselaphognatha indicates a neurological plasticity which is able to call forth inter-segmental combinations of movements and paired leg relationships in great variety just as they are required. There is no indication that the potentialities of the nervous system become limited with specialization of habits. The conspicuous morphological features of the trunk to which reference has been made in this and in previous parts may facilitate some types of gait and exclude others, but they do so for mechanical and not for neurological reasons.

THE SUPPOSED PRIMITIVENESS OF THE PSELAPHOGNATHA.

Verhoeff (1926), in support of his view that 'die Pselaphognathen unter den rezenten Diplopoden als die primitivsten organisierten', refers to rings 2-4 being indistinguishable in their tergites, pleurites and sternites from the hinder diplo-segments. If this uniformity is primitive no satisfactory functional reasons can be advanced to account for the absence of one pair of legs on rings 2-4. If, on the other hand, the ancestors of the Pselaphognatha rolled up, then the missing anterior legs receive a clear explanation (Part 4, p. 349), and if rolling up was later abandoned, as suggested above, the special requirements of the anterior rings would also be lost. Since all legs must take equal strides if they are to be equally efficient, the presence of legs of almost equal length on all rings, and a uniformity in the rings, is advantageous. The anterior legs of many Juliformia are frequently little used for walking (see Part 4, Pls. 52 and 53, figs. 11, 25 and 26), and such a condition in a shorter-bodied animal would be undesirable, and particularly so when walking upside down, as too much of the anterior end of the body might be momentarily unsupported. The condition of rings 2-4 in *Polyxenus* therefore may not be primitive, but secondarily adapted to present habits after protective spiralling had been abandoned.

The ratio of length to breadth of the body in arthropods is very various, and that of *Polyxenus* is more like the various hexapods and the shorter Chilopoda and Paupoda than the majority of Diplopoda (Part 4, p. 345). Since a longish but not

extremely long body is advantageous in supplying power for pushing in the Diplopoda (see Part 4, pp. 346, 348 and 359), the absence of this need in *Polyxenus* removes an advantage in possessing a long series of rings. Living on ceilings is controlled by the adhesive ability of the legs, and a longer body with more rings will not make running upside down any easier. It is probable that ancestral millipedes when acquiring their diplo-segments may have shown the same overall shape as seen in the majority of Diplopoda living today, and if so, they probably had more rings than are present in *Polyxenus*. Thus it is probable that the Pselaphognatha have secondarily reduced the length of their bodies as a result of giving up the pushing habit. A secondary reduction in the number of rings is probable in members of some other groups of Diplopoda, but associated with different needs (see Part 4, pp. 358, 362, etc.).

The Pselaphognatha have perhaps one claim to primitiveness in the absence of gonopods. If these specialized limbs have never been present, it suggests that the Pselaphognatha separated from the ancestral diplopod stem after diplo-segments were established and before gonopods were evolved, and gonopods may well have appeared independently in the several diplopod orders. Gonopods also might hinder upside down running if few legs are present.

CONCLUSIONS.

The structural features grouped under the headings 1-18 above, those mentioned in the preceding section, together with the locomotory features, indicate that the Pselaphognatha are one of the most specialized of diplopodan orders. The correlations which have been shown to exist between structure and habits of the Pselaphognatha, and of other millipedes, supply an adequate explanation on a functional basis for most of the conspicuous trunk peculiarities of the Pselaphognatha. These animals appear to have separated early in diplopod evolution, and to have abandoned the basic diplopodan habits. No support is found for the suggestion (Heathcote, 1889) that *Polyxenus* represents an intermediate between Diplopoda and Chilopoda. The superficial similarity between the leg movements of *Polyxenus* and of epimorphic Chilopoda is noticeable even if the gaits of neither are fully understood, and an appreciation of this resemblance has doubtless led naturalists to suggest chilopodan affinities of the Pselaphognatha.

This study of *Polyxenus* has shown how far reaching are the correlations between structure and habits. Although the data presented in Parts 3 and 4 are less detailed, it is probable that similar correlations exist in all Myriapoda. Almost all the anatomical features of the trunk of *Polyxenus* here described must be concerned with survival, and must therefore be subject to continual pressure by environmental selection, and the range of variation in these features may be limited by this means. The gonopods of Diplopoda contrast with the trunk features considered here and in Part 4 in their greater range of form, much of which appears to be extravagant and non-functional. Blower will suggest in a future publication (Ray Society Monograph) that the gonopods, which arise late in the life history, are not subject to the same type of environmental pressure as effects the trunk features considered above, and provided the gonopods perform their essential function, wide variation may not be eliminated by selection.

The habits which appear to have been of importance in directing the morphological evolution of the Pselaphognatha are not always exhibited by these animals. *Polyxenus* living in woodland soil may shelter on the ceilings of crevices, but in soil or among the roots of plants or on the leaves of trees the special proficiencies of the animal may not be exercised. A wide range of location becomes possible whenever predators and humidity allow, and it may be recalled that the Scolopendromorpha, for example, perform their maximum speeds with reluctance, and under many circumstances will not perform them at all, although this ability appears to be the one with which their structural evolution has been most closely associated. The capabilities of an animal which may have particular phylogenetic significance vary greatly in their

ease of recognition. The outstanding proficiencies of a whale or a giraffe are more obvious to us than are those of small animals whose detailed habitats are both variable and far removed from those of the higher vertebrates. When environmental conditions become easy a species may spread into a wide variety of places, but as soon as conditions become difficult, then special proficiencies may be called into play and determine survival. Bidder (1931) has drawn attention to the intermittent action of natural selection, discussing the extreme case of cataclysms and their importance in controlling evolution.

SUMMARY.

1. The habits of *Polyxenus lagurus* and the locomotory mechanism and skeletal-muscular systems which make these habits possible are described.

2. It is suggested that the circumstance and the habit which have been of greatest significance in directing the evolution of the Pselaphognatha are : small size (which renders burrowing by pushing less effective than in larger millipedes); and an ability to live on smooth ceilings of crevices (where many predators cannot easily follow), although this habit is not always exercised, pp. 180 and 183.

3. The structure and mode of adhesion by the tarsal claw are described. The adhesive lappet of *Polyxenus* is considered to be a refinement enabling glass-smooth surfaces to be negotiated, and not to be a feature upon which the whole evolution of the Pselaphognatha has depended.

4. The components of the exo- and endoskeleton are very light, basically diplopodan in nature, and highly specialized in detail. The internal transverse segmental tendons corresponding to every pair of legs is a feature commonly found in Crustacea, but restricted to the head in other Diplopoda (mandibular adductor tendon, etc.) and the V- and Y-shaped skeletal bars are unique.

5. The sheets of trunk muscles seen in other Diplopoda are represented in *Polyxenus* by an elaborate series of penicilli which appear to have evolved from the basic diplopodan pattern. Some cause movement, others by their tone stabilize skeletal units, and the muscular system is quite unlike that of a primitively soft-bodied arthropod.

6. The structure of the cuticle is described : the soft body is shown to be a specialization enabling the rings to be telescoped (in contrast to other Diplopoda), and the pleural lobes and posterior spine bundles to be moved.

7. Provisions for defence against predators and water are described : they include the flatter shape, the structure and distribution of spines and spinules, telescoping and local body movements.

8. Specializations connected with the ability to live on the ceiling of a hide involve details of the whole trunk region and are listed under 1-18 on pp. 180-181.

9. The movable part of the leg obtains an advantageous lateral origin by the form and immobility of the coxa. Unique extrinsic promotor and remotor muscles operate from the pre-femur. The limbs are not as short as in some Juliformia yet are under cover by the spines at all times.

10. *Polyxenus* is relatively fast moving, and obtains speed by using a larger angle of swing and quicker stepping than other Diplopoda.

11. The pattern of the gait (4.0 : 6.0)-(0.5 : 9.5) or slower, at phase differences between successive legs of 0.8-0.6, is remarkable in that speed is obtained from a slow pattern of gait, and that the phase differences between successive legs resembles those of the epimorphic Chilopoda and not the Diplopoda. Both features are shown to be obligate mechanical necessities.

12. The phase difference between legs of a pair is 0 in the slower gaits and increases to 0.5 in the faster gaits. Functional reasons are given for this curious combination of paired legs moving out of phase and a 'bottom gear' gait.

13. It is concluded that the Pselaphognatha are one of the most specialized orders of Diplopoda, showing neither primitive diplopod features nor characters primitively

intermediate between Chilopoda and Diplopoda. Gait resemblances to Chilopoda are partial, and are the obligate result of using a large angle of swing with a diplopod type of gait executed by as small a number as 13 pairs of legs.

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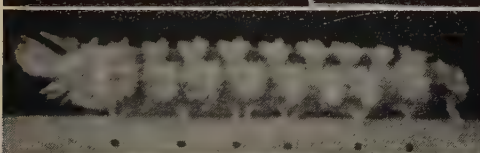
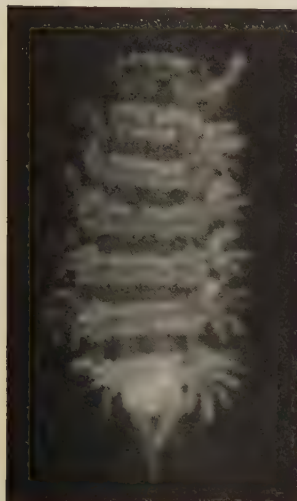
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KEY TO TEXT-FIGS. 1, 2, 3.

- | | | | |
|-----------------------------|---|--|---|
| a. | arm of transverse segmental tendon. | l. | oblique muscle from apex of V-shaped skeleton to outer ramus of the preceding Y-shaped skeleton. |
| a.s. | musculus apophysis sternalis. | | |
| a.s.a., a.s.b., a.s.c. | parts of musculus apophysis sternalis. | l.2-l.10. | legs 2-10 respectively. |
| a.te.s. | anterior row of tergal spines. | l.r. | ramus of Y-shaped skeleton lying along the leg. |
| b. | median part of transverse segmental tendon. | lev.po.fe. | levator postfemoris. |
| cox. | coxa. | m. | oblique muscle from apex of V-shaped skeleton to inner ramus of Y-shaped skeleton in front. |
| cox.l.2, cox.l.6. | coxa of legs 2 and 6 respectively. | | |
| d. | muscle from origin of tracheal pouch to pleural lobe. | n. | oblique muscle from arm of V-shaped skeleton to outer ramus of Y-shaped skeleton behind |
| d.s.a. | dorso-sternal muscle to transverse tendon. | . | |
| d.s.b. | dorso-sternal muscle to outer ramus of Y-shaped skeleton. | n.c. | nerve cord. |
| d.s.c. | dorso-sternal muscle to outer edge of coxa. | o. | oblique muscle from tergite to inter-tergite arthrodial membrane. |
| d.s.l.8, d.s.l.9, d.s.l.10. | dorso-sternal muscles of legs 8, 9 and 10 respectively. | o.t.p. | external opening of tracheal pouch. |
| d.s.te. | attachment of dorso-sternal muscles to tergite. | p. | muscle from dorso-sternal group Y to antero-lateral corner of following tergite. |
| dep.fe. | depressor femoris. | p.te.s. | posterior row of tergal spines. |
| dep.po.fe. | depressor postfemoris. | pl. | pleurite. |
| dep.pr.fe. | depressor prefemoris. | pl.a.w. | attachment of transverse muscle w from two segmental tendons to lower edge of pleurite. |
| e. | muscle from posterior edge of coxa to tracheal pouch. | pl.1, pl. 2, pl.3, pl.4 (l.4 and 5), pl.5 (l.6 and 7), pl.6. | pleural lobes or spine rosettes 1-6 with their corresponding legs. |
| e.cox.5, e.cox.6. | proximal margin of coxa of legs 5 and 6 respectively. | po.fe. | postfemur. |
| e.r. | external ramus of Y-shaped skeleton. | pr.fe. | prefemur. |
| f. | muscle from arthrodial membrane to pleural lobe. | prot.fe. | protractor femoris. |
| f.t. | flexible cuticle between tergite and pleurite. | prot.pr.fe. | protractor prefemoris. |
| f.7.a.-f.7.l. | position of sections shown in text-figs. 7a-l respectively. | q. | muscle from dorso-sternal group Y to lateral edge of succeeding tergite. |
| f.8.n.-f.8.r. | position of sections shown in text-figs. 8n-r respectively. | r. | muscle from dorso-sternal group X to lateral edge of tergite. |
| fe. | femur | ret.dor. | retractor dorsalis. |
| fl.ext.dor. | flexor externus dorsalis. | ret.fe. | retractor femoris. |
| fl.int.dor. | flexor internus dorsalis. | ret.pr.fe. | retractor prefemoris. |
| fl.ti.tar. | flexor tibiae tarsi. | ret.par. | retractor paratergalis. |
| fl.un. | flexor unguiculi. | s. | muscle from dorso-sternal group Y to antero-lateral edge of tergite. |
| g. | transverse muscle from posterior part of tergite to arthrodial membrane. | t. | muscle from dorso-sternal group X to antero-lateral edge of preceding tergite. |
| gen. | genital opening. | t.p. | muscle from lower margin of tergite to ventral side of pleural lobe. |
| h. | heart. | t.p.5 (p.t.p.), t.p.6 (a.t.p.). | tracheal pouch of leg 5 (posterior tracheal pouch of ring 5) and tracheal pouch of leg 6 (anterior tracheal pouch of ring 6). |
| i. | muscle from dorso-sternal group to anterior margin of coxa. | | |
| i.m. | inter-tergite arthrodial membrane. | | |
| i.r. | inner ramus of Y-shaped skeleton. | | |
| int. | intestine. | | |
| k. | transverse muscle from middle of segmental tendon to pedigerous lamina between successive legs. | | |



Polyxenus lagurus.

<i>ta.1., ta. 2.</i>	tarsus 1 and tarsus 2 respectively.	<i>u.</i>	muscle from transverse tendon to pleural lobe.
<i>te.</i>	tergite.	<i>v.</i>	V-shaped skeleton.
<i>te.a.</i>	anterior thickened rim on tergite.	<i>w.</i>	transverse muscle from transverse tendon to ventral edge of pleurite.
<i>te.a.e.</i>	lateral extent of anterior rim on tergite.		
<i>te.e.</i>	lateral edge of tergite.		
<i>te.s. (l.1), te.s. (l.2), te.s. (l.3), te.s. (l.4 and 5).</i>	spines of tergites corresponding to legs as numbered.	<i>X.</i>	anterior group of dorso-sternal muscles passing to posterior leg of the same ring.
<i>te.6, te.7.</i>	tergite of rings 6 and 7 respectively	<i>Y.</i>	posterior group of dorso-sternal muscles passing to anterior leg of succeeding ring.
<i>ti.</i>	tibia.		
<i>tr.</i>	trochanter.		
<i>tr.p.</i>	tracheal pouch.	<i>z.</i>	muscle from transverse segmental tendon to ventral side of pleural lobe.
<i>st.</i>	triangular part of pedigerous lamina surrounded by folds.		

DESCRIPTION OF PLATE 5.

The black or white spots mark groups of legs in contact with the ground, and their distance apart roughly indicates the stride length: 'p.d.' denotes the phase difference between each leg and the leg in front.

FIGS. 9–17. Living *Polyxenus lagurus*.

FIG. 9. Fourth instar (7 rings, 6 pairs of legs), length 0.9 mm. (posterior setae damaged). $\times 56$.

FIGS. 10 and 11. The same adult animal: fig. 10, walking slowly, turning and longitudinally contracted and fig. 11, fast walking at maximum extension of 3.2 mm. $\times 21$.

FIGS. 12 and 13. 4 mm. adult in ventral view walking fast on glass, the gait in both is (4.0 : 6.0), p.d. 0.8 approx. and stride length 1.0–1.06 mm.; fig. 12, the paired legs are in the same phase, right legs on the ground: 1 and 2; 5, 6 and 7; 10, 11 and 12; right legs off the ground: 3 and 4; 8 and 9; and 13. $\times 14.5$; fig. 13, the paired legs show a phase difference of 0.3, right legs on the ground: 1; 3, 4 and 5; 8, 9 and 10; and 13; right legs off the ground: 2; 6 and 7; 11 and 12. $\times 14.5$.

FIGS. 14–17. Lateral views of adult 4 mm. long walking on a cylindrical grass stem. $\times 14.5$.

FIG. 14. Walking slowly by gait (2.0 : 8.0), p.d. 0.65 (see text-fig. 5 *d*), legs on the ground: 1; 2 and 3; 4 and 5; 6 and 7; 9 and 10; 12 and 13; legs off the ground: 8; and 11; stride length 0.55 mm.

FIG. 15. Walking faster by gait (3.0 : 7.0), p.d. 0.75 (see text-fig. 5 *c*), but anterior legs with a smaller p.d., legs on the ground: 2 and 3; 4, 5 and 6; 8, 9 and 10; 12 and 13; legs off the ground: 1; 7; and 11: left leg 1 in opposite phase to right leg 1, stride length 0.85 mm.

FIG. 16. Walking faster by a gait near (4.0 : 6.0), p.d. 0.8 (see text-fig. 5 *b*), but anterior legs with a smaller p.d.; legs probably on the ground: 2, 3 and 4; 6, 7 and 8; 11, 12 and 13; legs probably off the ground: 1; 5; 9 and 10; stride length 1.06 mm.

FIG. 17. Animal walking upside down, gait between (4.0 : 6.0) and (3.0 : 7.0), p.d. 0.8–0.75.

FIG. 18. Frontal section through pleurite and rosette of spines, and anterior margin of succeeding tergite in lower right-hand corner. $\times 260$.

FIG. 19. Transverse section through tergite passing transversely through spines of the posterior row of the preceding tergite and showing spinules. $\times 260$.

FIG. 20. Frontal section through pleurite showing spinules. $\times 900$.

JOURNEY TO NORTHERN ETHIOPIA (SIMIEN), 1952-3: COLEOPTERA, CARABIDAE. By P. BASILEWSKY, F.R.E.S., Musée Royal du Congo Belge, Tervuren. (Communicated by HUGH SCOTT, Sc.D., F.R.S., F.L.S.)

(With 7 text-figures.)

[Read 19 January 1956.]

Après avoir exploré le Chillalo en 1926, puis le Gughé en 1948, le Dr. Hugh Scott a parcouru, les derniers mois de 1952, le haut massif du Simien, au nord du lac Tana. Les matériaux entomologiques qu'il a recueillis dans cette région sont particulièrement intéressants et complètent très heureusement ses précédentes récoltes. Grâce aux expéditions du Dr. Scott nous possédons maintenant des données importantes sur le peuplement entomologique de divers massifs abyssins, aussi bien au Nord qu'au Sud de ce pays. Ce sont les seules données, d'ailleurs, qui offrent suffisamment de précisions quant à la localité et à l'altitude, et c'est ce qui augmente considérablement leur intérêt.

Je tiens à remercier très chaleureusement le Dr. Hugh Scott d'avoir eu l'obligeance de me soumettre les Carabidae qu'il a recueillis au Simien et qui se sont avérés particulièrement intéressants. Le Dr. R. Jeannel a consacré une étude spéciale (1954) aux *Trechus* de ce massif. Le Dr. S. L. Straneo a bien voulu se charger de l'examen des quelques Pterostichinae recueillis. Les *holotypes* des nouveautés se trouvent au British Museum (Natural History); les *paratypes* dans la même institution et au Musée Royal du Congo Belge à Tervuren.

Bien que près de 900 Carabidae (*Trechinae* et *Pterostichinae* exclus) aient été recueillis par le Dr. Scott au Simien, cette collection ne renferme que 23 espèces, ce qui dénote une certaine pauvreté qualitative.* Cette pauvreté est peut-être due au fait que ces Insectes ont été récoltés surtout entre 10,000 et 14,000 pieds, donc en pleine zone alpine; seules les formes alticoles ou pouvant supporter une telle altitude ont été rapportées. Mais cette circonstance augmente considérablement l'intérêt de la collection.

Sur ces 23 espèces, cinq se sont avérées nouvelles, toutes alpines et particulièrement intéressantes. Un *Omotaphus*, qui n'offre d'affinités qu'avec une forme de l'Aberdare et de l'Elgon; un *Liagonum* très caractéristique, se rapprochant d'une espèce du Kilimandjaro; trois *Calathus* inédits. À ce propos, il est important de faire remarquer qu'aucun *Calathus* déjà connu d'Abyssinie n'a été retrouvé au Simien, nous nous trouvons donc en présence d'un endémisme bien marqué, semblable à celui des *Trechus* de la même région, car le Dr. Jeannel a dénombré, parmi les exemplaires récoltés du Dr. Scott, sept espèces différentes, toutes inédites.**

En plus de ces nouveautés, j'ai eu la grande joie de retrouver trois espèces, connues seulement par les types et provenant du Nord de l'Abyssinie, qui n'avaient plus été recueillies depuis leur première découverte par Raffray: notamment *Amara fairmairei* Raffray (décrit du Mont Abouna-Yousef), *Chlaenius dinodoides* Chaudoir (décrit d'Adoua) et *Afrotarus raffrayi* Fairmaire (décrit des montagnes du Lasta). Ces espèces sont donc probablement étroitement localisées.†

* Including the seven species of *Trechus* described by Dr. Jeannel, the single species of *Abacetus* (below, p. 192) and an undetermined *Philorhizus* (below, p. 202), the Carabidae collected total 32 species.—H. S.

** The reference to M. Basilewsky's earlier paper (1953), on the Carabidae collected in the Gughé Highlands and elsewhere in Southern Ethiopia in 1948-9, will be found in the Bibliography on p. 202.—H. S.

† Notes on the localities where these species were originally discovered are given at the foot of pp. 201, 202.—H. S.

Subfam. *CARABINAE*.*Caminara chlorostictum* (Dejean).*Carabus rugosus* De Geer, 1783.*Calosoma rugosum*, var. *chlorostictum* Dejean, 1831.

SIMIEN : Derasghié, c. 9,800 ft., 24. xii. 1952, 1 ♂ (Dr. R. Jeannel det.). " Cet exemplaire se trouvait solitaire dans les herbes à côté de la tente. Malgré de minutieuses recherches et des promesses de récompense aux indigènes, aucun autre spécimen n'a pu être trouvé " (Scott).

Cette espèce est largement répandue en Afrique australe et orientale, du Cap à l'Érythrée ; commune en Égypte, elle se rencontre également en Arabie. La ssp. *helenae* Hope est spéciale à l'île de Sainte-Hélène et la ssp. *coognatum* Chaudoir ne se trouve que dans l'archipel du Cap Vert.

Subfam. *SCARITINAE*.*Clivina natalensis* Putzeys, 1863.

TACAZZÉ RIVER: near bridge, c. 2,600 ft., 24. i. 1953, from stony bed of river, 10 ex.

Espèce très largement répandue dans toute l'Afrique Orientale, Centrale et Australe, mais ne se rencontrant guère au dessus de 2,000 mètres.

Subfam. *BEMBIDIINAE*.*Omotaphus mixtus* Schaum, ssp. *tropicus* Chaudoir.

SIMIEN : ravine on W. side of Mai Shaha valley, c. 9,000 ft., 14. xii. 1952, 2 ex.

O. mixtus est largement répandu en Afrique Orientale, Centrale et Australe, de même qu'à Madagascar, en Arabie, en Égypte et en Syrie. La forme *tropicus* est une race alticole propre à l'Éthiopie, caractérisée par les élytres plus sombres, à taches jaunes plus floues et moins marquées, parfois tout à fait effacées, et avec seulement le premier article des antennes clair. Cette forme se rencontre sur tous les massifs éthiopiens, à partir de 3,000 mètres d'altitude. Dr. Scott l'a déjà capturée sur le Chillàlo (1926) et le Gughé (1948).

Omotaphus simienensis, sp. nov.

Long. 2,5-3,8 mm.

Dessus d'un noir bronzé métallique brillant, les élytres moins foncées que l'avant-corps, pourvus d'une petite tache jaune à l'épaule même et mal limitée, et de deux taches postérieures, l'une zigzaguant de l'angle apical externe jusqu'à la première strie et plus large vers l'extérieur, l'autre occupant les trois premiers intervalles et située un peu avant l'apex ; chez de nombreux exemplaires le disque de l'élytre est éclairci et d'un brun bronzé. Dessous noir de poix brillant ; pattes d'un brun variablement testacé ; antennes brunes, à premier article plus clair ; palpes bruns, à dernier article testacé.

Microsculpture très serrée et formant des mailles polygonales.

Cette nouvelle espèce est voisine d'*O. altipeta* Alluaud, de l'Aberdare et de l'Elgon, à partir de 2,500 m., et en diffère par les caractères suivants : angles postérieurs du pronotum aigus et saillants chez *simienensis*, subdroits chez *altipeta*. Élytres ovoïdes chez *altipeta*, et à épaule peu marquée et très arrondie, tandis que chez la nouvelle espèce ils sont plus parallèles, à épaule bien marquée et peu arrondie. Stries élytrales plus profondes et plus larges chez la nouvelle espèce. La tache postérieure, n'occupant chez *altipeta* que les intervalles 6 à 9, est ici beaucoup plus étendue et va en zigzaguant de l'angle apical externe jusqu'à la première strie.

O. simienensis semble être localisé sur le Simien entre 9,000 et 13,000 pieds, mais surtout abondant à cette dernière altitude.

SIMIEN : ravine on W. side of Mai Shaha valley, c. 9,000 ft., 14. xii. 1952, 1 ex. ; near Encheteab, over 9,000 ft., 25. xii. 1952, beneath large stones round drinking pool for cattle, 21 ex. ; Debarec, c. 9,800 ft., 11. xi. 1952, from streams with steep earth banks and small water-falls, 1 ex. ; near Mindigabsa, over 10,000 ft., 16. xi. 1952, from stiff wet mud or under stones in bed of torrent, 43 ex., and 9 other specimens from dry soil in roots of tufted plants overhanging a stream ; Mecana torrent, below Mecana-Abbo, c. 10,000 ft., 9. xii. 1952, 35 ex. ; below Atgheba Ghiyorghis, c. 10,500 ft., 7. xii. 1952, from wet rocks below a spring, 1 ex. ; Lori, c. 11,500 ft., 25-27. xi. 1952, 2 ex. ; slopes above Lori, c. 12,000 ft., 28. xi. 1952, from soil at base of a dead stem of *Lobelia rhynchopetalum*, 1 ex. ; Aostagheb, c. 11,500 ft., 20. xi. 1952, beneath rocks sunk in turf, 1 ex. ; Arghine, c. 11,500 ft., 23. xi. 1952, near stream in ravine, 44 ex. ; Mai Datcha (E. of Arcuasié), c. 13,200 ft., 5. xii. 1952, from beneath stones and radical leaves of the Composite *Landtia rueppellii*, on marshy ground, 163 ex. (among them the *holotype*), as well as 3 other specimens from the floor of the valley.—Nombre total d'exemplaires : 325.

Holotype au British Museum (Natural History) ; *paratypes* dans la même institution et au Musée Royal du Congo Belge à Tervuren.

Bien qu'assez proche d'*O. altipeta*, je considère *O. simienensis* comme espèce distincte et non comme une race géographique du premier, et cela pour des raisons plus géographiques que morphologiques et qui ont été exposées précédemment (Basilewsky, Révision des genres *Hystrichopus* Boh. et *Plagiopyga* Boh., *Ann. Musée Roy. Congo Belge*, sér. in-8°, Zool., 31, pp. 17-18, 1954). L'édéage de la nouvelle espèce est peu différent de celui d'*O. altipeta* ; mais chez toutes les formes du genre *Omotaphus* l'organe copulateur ne présente que des différences relativement peu sensibles, et seule une étude d'ensemble de toutes les espèces et races permettra d'évaluer à sa juste valeur l'importance spécifique ou subs spécifique de ces différences.

On peut scinder en 3 groupes les espèces du genre *Omotaphus*, d'après la microsculpture tégumentaire. Le premier, ne comprenant que *O. scotti* Netolitzky, est caractérisé par cette microsculpture absente ou du moins indistincte même à très fort grossissement ($\times 180$), sauf à la partie postérieure de la tête. Chez les formes du second groupe (*O. mixtus* Schaum, ssp. *tropicus* Chaudoir, et ssp. *kivuanus* Basilewsky), cette microsculpture est présente et bien marquée, mais forme sur les intervalles des élytres des mailles nettement étirées en travers. Enfin, chez le troisième groupe, la microsculpture est encore plus forte et forme des mailles bien polygonales ; ce dernier groupe comporte les espèces suivantes : *sperans* Netolitzky (Damaraland), *mellissi* Wollaston (I. Sainte-Hélène), *kilimanus* Alluaud (Kilimandjaro), *altipeta* Alluaud (Elgon et Aberdare) et *simienensis*, sp. n. (Simien). J'avais considéré jusqu'à présent, avec Alluaud, *altipeta* comme une race de *mixtus*, mais la forte différence dans la conformation de la microsculpture élytrale chez les deux formes ne permet pas cette interprétation.

Peryphus scottustulatus (Netolitzky).

Bembidion (*Peryphus*) *scottustulatum* Netolitzky, *Ann. Mag. nat. Hist.* (10), 19, p. 413, 1937. *Peryphus atlanticus*, subsp. *adonawans* Basilewsky (nec Chaudoir), *J. Linn. Soc. (Zool.)*, 42, p. 279, 1953.*

SIMIEN : near Mindigabsa, over 10,000 ft., 16. xi. 1952, from stiff wet mud or under stones in bed of torrent, 1 ex. ; Arghine, c. 11,500 ft., 23. xi. 1952, near stream in ravine, 6 ex. ; ravine on W. side of Mai Shaha valley, c. 9,000 ft., 14. xii. 1952, 43 ex. ; Mecana torrent, below Mecana-Abbo, c. 10,000 ft., 9. xii. 1952, 81 ex. ; massif of Ras Degien, above Mecana-Abbo, c. 12,000 ft., 11. xii. 1952, from dry soil at base of *Lobelia rhynchopetalum*, 1 ex.—Nombre total d'exemplaires : 132.

* Bibliographic references to well known and widely distributed species are not given in every case. But the author has kindly furnished the principal references concerning species characteristic of Ethiopia, or known only from that country.—H. S.

Espèce décrite par Netolitzky, en 1937, sur 2 exemplaires recueillis par le Dr. Scott en 1926 dans la Jem-Jem Forest, c. 8,000 ft. Le même récolteur la retrouva en 1948 sur le Gughé, et c'est erronément que je l'ai désignée sous le nom d'*adovanus* Chaudoir dans mon étude sur les Carabiques de cette région publiée en 1953. Ainsi que j'ai pu m'en convaincre depuis, le vrai *adovanus* diffère très nettement de l'espèce de Netolitzky par la partie postérieure de la tête fortement ponctuée.

Peryphus muscicola Basilewsky.

Peryphus muscicola Basilewsky, *J. Linn. Soc. (Zool.)*, **42**, p. 278, 1953.

SIMIEN : Mecana torrent, below Mecana-Abbo, c. 10,000 ft., 9. xii. 1952, 77 ex. ; near Mindigabsa, c. 10,000 ft., 29. xii. 1952, 1 ex. ; east of Mindigabsa, over 10,000 ft., 16. xi. 1952, from dry soil in roots of tufted plants overhanging a stream, 4 ex., and from stiff wet mud or under stones in bed of torrent, 4 ex. —Nombre total d'exemplaires : 86.

J'ai décrit récemment cette espèce sur de nombreux individus recueillis par le Dr. Scott dans l'Éthiopie méridionale, sur le Mt. Damota, à une altitude identique. Les spécimens que j'ai actuellement sous les yeux diffèrent légèrement de la série typique par les pattes d'un testacé plus ou moins clair uniforme.

P. muscicola a, comme *P. melanocerus* Chaudoir, la tête imponctuée, contrairement aux formes du groupe *atlanticus*. Elle en diffère par le pronotum plus fortement ponctué à la base, par les dépressions basilaires pronotales plus profondes et plus arrondies, par les points des stries élytrales plus profonds et plus gros et par la microsculpture des élytres formant un réseau bien plus régulier, bien que composé de mailles également transversales.

Tachyura conspicua (Schaum, 1863).

TACAZZÉ RIVER: near bridge, c. 2,600 ft., 24. i. 1953, from stony bed of river, 1 ex. Espèce d'Afrique Orientale et Australe, assez commune aux basses altitudes.

Tachyura longior Burgeon, 1935.

SIMIEN : camp near Mecana-Abbo, c. 10,500 ft., 12. xii. 1952, from stiff damp soil beneath boulders sunk in turf, 5 ex.

Espèce décrite du Congo Belge, mais que je connaissais aussi du Cameroun et de l'Aïr (Afrique Occidentale Française), encore jamais signalée de l'Éthiopie. Ces cinq spécimens sont entièrement d'un noir brillant.

Tachyura fausta (Péringuey, 1896).

SIMIEN : near Dabat, from valley S. of Falasha Mission, c. 7,000 ft., 21. i. 1953, 3 ex.

Espèce largement répandue en Afrique Orientale, Centrale et Australe, déjà recueillie par le Dr. Scott dans la Sidamo Province.

Tachyura spuria (Péringuey, 1896).

Tachys spurius Péringuey, *Trans. S. Afr. Phil. Soc.*, **7**, pp. 593, 596, 1896 ; Netolitzky, *Ann. Mag. nat. Hist.* (10), **19**, p. 419, 1937 ; Britton, *Brit. Mus. (Nat. Hist.) Exp. S. W. Arabia* 1937-8, **1** (10), p. 103, 1949.

Tachyura spuria Basilewsky, *J. Linn. Soc. (Zool.)*, **42**, p. 280, 1953 ; *id.*, *Rev. Zool.-Bot. Afr.*, **50**, p. 130, 1954.

Tachys metrius Alluaud, *Miss. Sci. Omo*, **5** (Zool.), p. 7, 1939.

SIMIEN : Debarec, c. 9,800 ft., 11. xi. 1952, beneath cracked surface of damp clay beside a stream, 2 ex.

Espèce d'Afrique Orientale, Centrale et Australe, déjà recueillie par le Dr. Scott en Éthiopie, en 1926-27 et en 1948.

Subfam. *PTEROSTICHINAE*.*Abacetus germanus* Chaudoir.

SIMIEN : near Dabat, from valley S. of Falasha Mission, c. 7,000 ft., 21. i. 1953.
5 ex.

Cette espèce a été identifiée par mon cher ami le Dr. S. L. Straneo, de Gallarate (Italie), l'éminent spécialiste des *Pterostichinae*. La forme typique est connue d'Éthiopie, mais l'espèce est représentée par des sous-espèces dans plusieurs régions de l'Afrique tropicale.

Subfam. *ANCHOMENINAE*.*Liagonum scotti*, sp. nov. (Fig. 1.)

Long. 10,5 mm.

Aptère. Tout le dessus d'un brun ferrugineux assez brillant ; dessous, pattes, palpes et antennes d'un brun un peu plus clair.

Tête volumineuse et massive, assez large, les yeux peu gros et modérément saillants, les tempes longues et obliques, à peine bombées, glabres ; soie orbitale postérieure nettement déportée en arrière. Labre court et large, à bord antérieur très faiblement bisinué, le milieu un peu avancé. Surface imponctuée, à microsculpture isodiamétrale polygonale bien marquée, avec une légère dépression longitudinale latérale sur le clypéus et l'avant du front. Dent labiale courte et large, aiguë au sommet. Antennes assez longues, dépassant la base du pronotum de près de 3 articles, le troisième de même longueur que le quatrième, glabre.

Pronotum plus large que long, transversal, peu convexe, nettement cordiforme à largeur maximale déportée en avant du milieu ; bord antérieur subdroit, les angles antérieurs bien marqués et bien séparés du cou mais nullement saillants vers l'avant en larges lobes arrondis ; côtés arrondis et élargis jusqu'à la largeur maximale qui se trouve à la fin du premier tiers, ensuite rétrécis en courbe régulière jusqu'à la fin du second tiers, puis redressés et rectilignes jusqu'aux angles postérieurs qui sont droits et arrondis au sommet, formant une sinuosité assez longue ; base droite, bien plus étroite que le bord antérieur ; sillon longitudinal médian fin mais assez long, n'atteignant cependant ni le bord antérieur ni la base ; côtés largement explanés, relevés surtout en arrière, la gouttière marginale plus profonde et plus large en arrière où elle se confond avec la dépression basilaire ; surface lisse et imponctuée, à microsculpture semblable à celle de la tête. Soie prothoracique antérieure située à l'endroit de la plus grande largeur, la postérieure un peu avant l'angle. Écusson petit, large, triangulaire et imponctué.

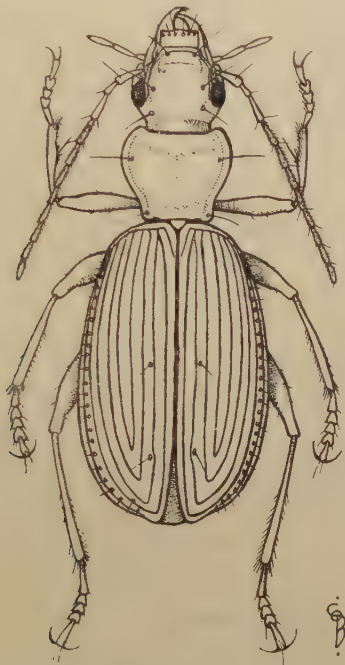
Élytres ovoïdes, un peu élargis en arrière (♀), la largeur maximale située tout au début du tiers postérieur ; disque déprimé ; épaule peu marquée et bien arrondie ; troncature fortement oblique et non sinuée, l'angle sutural bien arrondi, ni denté ni épineux ; stries peu profondes mais assez larges, à ponctuation bien distincte mais non serrée ; striole scutellaire courte et faible ; intervalles très plans, imponctués, à microsculpture formant un réseau serré de mailles polygonales et très petites ; troisième intervalle avec 2 pores dorsaux, le premier au milieu de la longueur, le second fortement en arrière. Série ombiliquée avec 23 fouets.

Dessous imponctué et glabre, les côtés de l'abdomen chagrinés ; apophyse prosternale non rebordée ; métépisternes plus longs que larges au bord antérieur. Soies abdominales normales présentes. Segment anal (♀) avec 8 soies. Pattes de longueur normale ; premiers articles des tarses postérieurs et intermédiaires fortement bisillonnés, le cinquième article non sétulé en dessous.

SIMIEN : Arghine, c. 11,500 ft., 23. xi. 1952, near stream in ravine, 2 ♀♀.

Holotype au British Museum (Natural History) ; *paratype* au Musée Royal du Congo Belge à Tervuren.

Dans le genre *Liagonum* cette nouvelle espèce ne se rapproche que de *L. jeanneli* Alluaud, du Kilimandjaro, mais en diffère au premier coup d'œil. En effet, *L. jeanneli* est beaucoup plus étroit, avec les épaules encore plus effacées, le pronotum non transversal et à peu près aussi large que long, encore plus fortement rétréci en arrière, les antennes plus longues, dépassant la base du pronotum de 4 articles, les yeux beaucoup plus gros et plus saillants, et le troisième intervalle des élytres avec 3 pores dorsaux au lieu de 2.



TEXT-FIG. 1.
Liagonum scotti, sp. nov. ($\times c. 6$).

Megalonychus shoanus Alluaud.

SIMIEN : Derasghié, c. 9,800 ft., 24. xii. 1952, from grassy valley near camp, 1 ex.

Espèce décrite d'Addis Ababa, mais largement répandue en Afrique Orientale et dans l'Est du Congo Belge.

Neobatenus mus (Basilewsky).

Probatenus mus Basilewsky, *J. Linn. Soc. (Zool.)*, **42**, p. 281, 1953.

SIMIEN : Derasghié, c. 9,800 ft., 22. xii. 1952, from grove of tall juniper-trees north of town, 1 ex. ; near Mindigabsa, c. 10,000 ft., 29. xii. 1952, from inflorescences of *Lobelia rhynchopetalum* or soil near by, 1 ex.

J'ai décrit cette espèce dans le genre *Probatenus*. Dans la classification des genres d'Anchomeninae que j'ai établie récemment (*Explor. Parc Nat. Upemba*, 10, *Carab.*, pp. 59-66, 1953), ce dernier est caractérisé par la microsculpture élytrale formant un réseau de mailles isodiamétrales. L'espèce dont il est question ici a ces mailles fortement étirées en travers et rentre, pour cette raison, dans le genre *Neobatenus*.

N. mus a été décrit du Mont Tola (massif du Gughé) ; les deux exemplaires du Simien ont des pattes très claires.

Gen. *CALATHUS* Bonelli.

Parmi les *Carabidae* recueillis au Simien par le Dr. Scott les *Calathus* sont particulièrement bien représentés : 282 exemplaires appartenant à trois espèces inédites. Ce fait est à rapprocher des résultats de l'étude du Dr. Jeannel des *Trechus* du même massif, sur lequel ont été trouvées sept espèces nouvelles et aucune de celles déjà connues d'autres montagnes d'Éthiopie. Nous constatons donc que les éléments d'origine paléarétique se montrent remarquablement endémiques sur le Simien, ce qui permettrait de nous livrer à d'intéressantes considérations sur le peuplement de ces régions alpines.

Tous ces *Calathus* ont été pris entre 9,800 et plus de 14,000 pieds, le plus souvent sous des pierres près des cours d'eau et dans les troncs de *Lobelia rhynchopetalum*, ou sous l'écorce de *Hagenia*, ainsi que sur des genévriers. D'un autre côté, les trois espèces semblent plus ou moins cohabiter, ce qui se présente également chez quelques uns des *Trechus* décrits par le Dr. Jeannel.

Dans le cadre de mon étude des *Carabidae* découverts sur le Gughé par le Dr. Scott, j'ai publié (1953, pp. 285-7) un tableau des espèces de ce genre connues à ce jour d'Afrique. Je donnerai plus loin quelques indications permettant d'incorporer les trois formes nouvelles dans ce tableau.

Calathus nitidus, sp. nov. (Fig. 2.)

Long. 7-8 mm.

Dessus très brillant dans les deux sexes, d'un brun de poix très foncé, la tête presque noire, les élytres faiblement irisés ; pourtour du pronotum légèrement éclairci ; dessous brun de poix, un peu plus clair au milieu : pattes et palpes d'un ferrugineux rougeâtre ; antennes brunes, les deux premiers articles testacés.

Tête assez large, les yeux moyens et très modérément saillants, les tempes longues et peu obliques ; surface lisse et imponctuée. Antennes longues, dépassant de trois articles la base du pronotum ; troisième article de même longueur que le suivant, à moitié distale pubescente.

Pronotum non transversal, à peu près aussi long que large, à largeur maximale fortement déportée en avant du milieu ; bord antérieur très faiblement concave, les angles antérieurs en lobes saillants mais largement arrondis au sommet ; côtés faiblement élargis et arrondis dans leur premier tiers jusqu'à l'endroit de la plus grande largeur, puis plus fortement rétrécis mais nullement sinués jusqu'aux angles postérieurs qui sont très largement arrondis et peu marqués ; base étroite, moins large que le bord antérieur ; sillon longitudinal particulièrement fin et peu marqué, très court ; dépressions basilaires à peine marquées ; gouttière marginale très étroite en avant, un peu élargie et explanée en arrière, mais à côtés non relevés ; rebord basilaire très incomplet. Surface lisse et imponctuée, à microsculpture peu nette.

Élytres ovoïdes et allongés, un peu plus larges chez la ♀, à largeur maximale située au milieu de la longueur, à disque nettement aplani ; épaule bien marquée mais sans denticule huméral ; stries légères et peu profondes mais entières, à ponctuation présente mais peu distincte ; intervalles plans, à microsculpture formant un réseau peu net de mailles étirées en travers, semblables chez les deux sexes ; troisième intervalle avec 8 pores dorsaux. Série ombiliquée comportant 23 fouets régulièrement alignés.

Dessous glabre et imponctué ; métépisternes courts et un peu transversaux. Édéage, fig. 2.

SIMIEN : Lori, c. 11,500 ft., 27-29. xi. 1952, from plateau near church of Kidana Mihrat, 3 ex. (including the *holotype*) ; slopes above Lori, c. 12,000 ft., 28. xi. 1952, from soil at base of dead stems of *Lobelia rhynchopetalum*, 2 ex. ; Arghine, c. 11,500 ft., 23-24. xi. 1952, near the torrent in the ravine, 3 ex. (one of these being found under stones and another in peat soil).—Nombre total d'exemplaires : 8.

Holotype au British Museum (Natural History); *paratypes* dans la même institution et au Musée Royal du Congo Belge à Tervuren.



TEXT-FIG. 2.

Calathus nitidus, sp. nov., édage ($\times 15$).

On pourra introduire cette espèce dans mon tableau des *Calathus* africains et en voir les affinités à l'aide des paragraphes suivants :

7. (8). Intervalle 3 des élytres avec 6 à 8 pores dorsaux.
- | | |
|---|--------------------------------|
| a. (b). Microsculpture élytrale formant un fin réseau de mailles polygonales très petites. Disque des élytres non aplani. Côtés du pronotum non sinués en arrière. Métépisternes non transverses, à peu près aussi longs que larges. Long. 6,5 mm.—Shoa | 3. <i>C. shoenus</i> Alluaud. |
| b. (a). Microsculpture élytrale formant un réseau moins net, avec des mailles étirées en travers. Disque des élytres aplani. Sinuosité postérieure des côtés du pronotum plus nette. Métépisternes un peu transverses. Long. 7-8 mm.—Simien | 3a. <i>C. nitidus</i> , sp. n. |

Calathus simienensis, sp. nov. (Fig. 3.)

Long. 7-9,5 mm.

Dessus d'un brun foncé, roux clair à l'avant de la tête, sur tout le pourtour du pronotum et à la base des élytres; dessous, pattes, antennes et palpes d'un roux ferrugineux. Tout le dessus brillant chez les deux sexes.

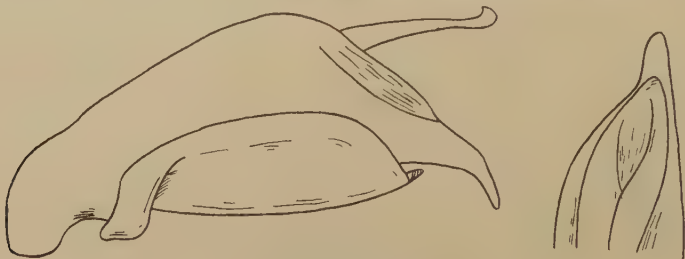
Tête allongée, les yeux modérément gros et médiocrement saillants, les tempes courtes, imponctuée et faiblement ridulée en travers. Antennes de longueur moyenne, ne dépassant la base du pronotum que de deux articles, le troisième un peu plus long que le suivant et ayant la moitié distale pourvue d'une pubescence assez faible.

Pronotum très transversal, bien plus large que long (1,45 fois), à largeur maximale située à peu près au milieu de la longueur et à la base, les côtés étant parallèles dans leur moitié postérieure; bord antérieur subdroit au milieu, oblique latéralement vers les angles antérieurs qui sont saillants vers l'avant mais arrondis au sommet; côtés élargis et arrondis dans la partie antérieure; angles postérieurs droits et arrondis au sommet; base subdroite, bien plus large que le bord antérieur; sillon longitudinal médian fin; dépressions basilaires presque indistinctes; gouttière marginale légèrement explanée, élargie en arrière où les côtés ne sont pas relevés; surface imponctuée; rebord de la base interrompu au milieu.

Élytres ovalaires, peu convexes, un peu élargis en arrière chez la ♀; denticule huméral bien marqué; stries bien marquées mais peu profondes, légèrement crénelées; intervalles tout à fait plans, à microsculpture isodiamétrale serrée et semblable chez les deux sexes, ce qui rend l'élytre aussi brillant chez le ♂ que chez la ♀; 3 soies dorsales sur le troisième intervalle. Série ombiliquée comportant 23 fouets disposés régulièrement et plus espacés au milieu.

Dessous glabre et imponctué; métépisternes très courts et très transverses, bien plus larges que longs. Édage, fig. 3.

SIMIEN : Derasghié, c. 9,800 ft., 22. xii. 1952, from grove of tall juniper-trees north of town, 99 ex. (including the *holotype*) : east of Mindigabsa, over 10,000 ft., 16. xi. 1952, near a torrent. 1 ex. : near Mindigabsa, over 10,000 ft., 17. xi. 1952, from crown of leaves of *Lobelia rhynchopetalum*, 11 ex. : same place, but six weeks later, 29. xii. 1952, from inflorescences of *Lobelia rhynchopetalum* or soil nearby, 5 ex. : Lori, c. 11,500 ft., 25-29. xi. 1952, from plateau near church of Kidana Mihrat, 87 examples (including 25 ex. found under dry bark of felled kosso-tree (*Hagenia abyssinica*) on 27. xi., and 3 ex. found at night on floor of lighted tent) ; slopes above Lori, c. 12,000 ft., 28. xi. 1952, from soil at base of dead stem of



TEXT-FIG. 3.

Calathus simienensis, sp. nov., édage ($\times 15$).

Lobelia rhynchopetalum, 1 ex. ; Arghine, c. 11,500 ft., 23-24. xi. 1952, 33 ex. (including 20 under stones near the torrent, and 2 under stones sunk in dry peat soil) ; Mai Datcha (E. of Arcuasié), c. 13,200 ft., 5. xii. 1952, from marshy valley, 31 ex. ; Ras Degien, below the Pass of Degien, over 14,000 ft., 11. xii. 1952, 1 ex. —Nombre total d'exemplaires : 269.

Holotype au British Museum (Natural History) : *paratypes* dans la même institution et au Musée Royal du Congo Belge à Tervuren.

Calathus ras, sp. nov. (Figs. 4, 5.)

Long. 9,5-10,5 mm.

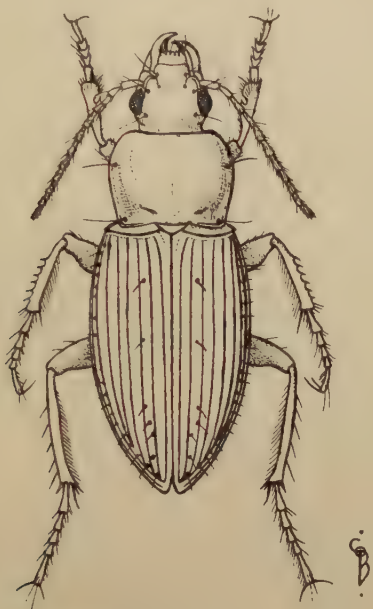
Dessus brun de poix, éclairci assez fortement sur le milieu de la tête. sur tout le pourtour du pronotum et à la base des élytres ; dessous brun de poix. plus clair au milieu ; pattes, antennes et palpes d'un ferrugineux rougeâtre. Avant-corps très brillant ; élytres brillants chez le ♂, mats chez la ♀.

Tête assez large et allongée, les yeux assez gros mais modérément saillants, les tempes longuement obliques ; surface imponctuée, sans ridulation, à microsculpture peu apparente. Antennes de largeur moyenne, ne dépassant guère la base du pronotum que de deux articles, le troisième un peu plus long que le quatrième, la moitié distale pubescente.

Pronotum très transversal, à peu près une fois et demie plus large que long, la largeur au milieu plus ou moins identique à celle de la base ; bord antérieur droit au milieu, ensuite remontant en oblique jusqu'aux angles antérieurs qui sont saillants vers l'avant mais arrondis au sommet ; côtés arrondis et élargis jusque vers environ la moitié de la longueur, ensuite rectilignes et parallèles jusqu'à l'angle postérieur qui est droit ; base bien plus large que le bord antérieur, à concavité à peine distincte, rebordée seulement latéralement ; sillon longitudinal médian fin et très court ; dépressions basilaires faibles et subarrondies ; gouttière marginale un peu explanée, fortement élargie en arrière où les côtés sont faiblement relevés ; surface imponctuée, à microsculpture isodiamétrale petite et très serrée.

Élytres ovoïdes, déprimés sur le disque, de même forme chez les deux sexes, à largeur maximale située à peu près au milieu ; un denticule bien marqué à l'épaule ; stries peu profondes et peu larges mais bien marquées sur toute leur longueur, à crénulation indistincte ; intervalles plans, à microsculpture isodiamétrale très fine et

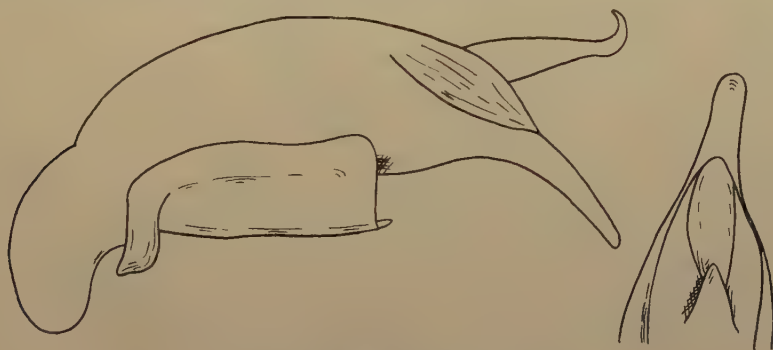
très serrée chez le ♂, à mailles plus larges et plus profondes chez la ♀, ce qui rend tout l'élytre mat chez ce dernier sexe : troisième intervalle avec 5 pores dorsaux. Série ombiliquée comportant 23 fouets, régulièrement alignés mais plus espacés au milieu.



TEXT-FIG. 4.
Calathus ras, sp. nov. ($\times c. 6$).

Dessous glabre et imponctué. Métépisternes petits et subcarrés, aussi longs que larges au bord antérieur. Édéage, fig. 5.

SIMIEN : slopes above Lori, c. 12,000 ft., 28. xi. 1952, from soil at base of dead stems of *Lobelia rhynchopetalum*, 1 ex. ; Ras Degien, below the Pass of Degien, 11. xii. 1952, 4 ex., of which three (including the *holotype*) were collected above 14,000 ft., while the fourth was taken, slightly lower down (c. 14,000 ft.), from a dead stem or inflorescence of *Lobelia rhynchopetalum*.



TEXT-FIG. 5.
Calathus ras, sp. nov., édéage ($\times 30$).

Holotype au British Museum (Natural History) ; *paratypes* dans la même institution et au Musée Royal du Congo Belge à Tervuren.

Ces deux espèces se rapprochent le plus de *C. vagestriatus* Fairmaire. Mon tableau des espèces africaines du genre devra être modifié comme suit afin de les contenir :

23. (24). Pronotum très transversal, une fois et demie plus large que long, largeur du milieu à peu près identique à celle de la base.
- a. (d). Élytres aussi brillants chez la ♀ que chez le ♂, par suite de la microsculpture semblable chez les deux sexes.
 - b. (c). Élytres plus ovoïdes et plus convexes, à striation plus faible, à microsculpture des intervalles plus nette. Métépisternes non transverses. Long. 7,5–10,5 mm.—Choa (Shoa) 11. *C. vagestriatus* Fairmaire.
 - c. (b). Élytres moins ovoïdes et plus ou moins déprimés sur le disque, à striation plus marquée, à microsculpture des intervalles moins marquée. Métépisternes très transverses. Long. 7–9,5 mm.—Simien 11a. *C. simienensis*, sp. n.
 - d. (a). Élytres du ♂ très brillants, ceux de la ♀ mats, par suite de la microsculpture des intervalles beaucoup plus forte chez ce dernier sexe. Long. 9,5–10,5 mm.—Simien 11b. *C. ras*, sp. n.

Subfam. ZABRINÆ.

Amara fairmairei Raffray. (Fig. 6.)

Amara fairmairei Raffray, Ann. Soc. Ent. France, (6) 5, p. 316, 1885.

Cette espèce fut décrite par Raffray sur un ou plusieurs spécimens recueillis par lui-même au Mont Abouna-Yousef, à 4.000 mètres d'altitude, sous des pierres. Il m'a été impossible d'en retrouver le type au Muséum de Paris, ce qui n'est guère étonnant, car la plupart des types des Carabidae d'Abyssinie décrits par Raffray restent introuvables. Une partie de ces insectes a été vendue par E. Deyrolle à F. Monchicourt, qui lui-même les a vendus à R. de Bonneuil. La collection de ce dernier a été recueillie par E. Le Moul et recédée à l'Institut royal des Sciences naturelles de Belgique à Bruxelles, mais aucun des types de Raffray ne s'y trouve. Que sont-ils devenus ? La plus grande incertitude règne, mais il est probable qu'on ne les retrouvera plus, soit qu'ils soient détruits, soit qu'ils figurent dans une collection quelconque mais sans aucune indication permettant de supposer qu'il s'agisse des spécimens de Raffray.

La petite série dont il est question ici ne se rapporte à aucune autre espèce connue, mais la description de *A. fairmairei* lui convient à merveille. Il est vrai que cette dernière est fort courte, mais l'auteur insiste sur la brièveté des élytres par rapport au pronotum, ce qui convient parfaitement à l'espèce que j'ai sous les yeux.

Plutôt que de considérer l'espèce de Raffray comme douteuse et de donner un nom nouveau à celle qu'a découverte le Dr. Scott, je préfère la cataloguer sous le nom de *fairmairei* et d'en donner une description détaillée, permettant facilement de la reconnaître. Si le type de Raffray venait un jour à réapparaître et si une comparaison avec celle que je décris montre qu'il s'agit de deux formes distinctes, un nom nouveau rectifiera vite cette fausse manœuvre. Mais comme il est beaucoup plus probable que ce type demeure inconnu, le nom de *fairmairei* pourra s'appliquer à celle que j'ai sous les yeux et un néotype pourra être choisi dans cette série.

Long. 7–8 mm. Espèce aptère. Corps court, très ovoïde et très trapu (*Rd*=2).

D'un bronzé obscur et brillant ; dessous brun de poix très foncé, l'abdomen plus clair ; pattes d'un ferrugineux rougeâtre foncé ; antennes brunes, les trois premiers articles testacés ; palpes bruns, l'extrémité du dernier article très claire.

Tête grosse et très large mais non transverse ; yeux gros mais modérément saillants ; tempes courtes ; cou très épais ; bord antérieur du clypéus légèrement échancré ; surface imponctuée ; suture clypéale peu marquée, avec un léger trait

longitudinal à l'extrémité : deux soies orbitales normalement situées. Dent labiale large et assez courte, bifide au sommet. Dernier article des palpes fusiforme, assez renflé dans la partie proximale : les labiaux polychètes. Antennes courtes et épaisses, n'atteignant pas la base du pronotum, les articles un peu sub-globuleux, le troisième plus long que le suivant, les trois premiers glabres.

Pronotum court et transverse, 1,8 fois plus large que long, assez convexe : bord antérieur droit au milieu, les côtés un peu obliques vers l'avant, l'angle antérieur légèrement saillant, non ou à peine arrondi au sommet, approchant fort de l'œil mais bien séparé du cou : côtés élargis et arrondis jusqu'à l'endroit de la largeur maximale, qui se trouve dans le quart postérieur, ensuite très faiblement rétrécis en courbe régulière mais peu prononcée, alors qu'elle est fortement marquée dans le premier tiers : angles postérieurs un peu obtus et largement arrondis : base droite, plus large que le bord antérieur, à rebord à peine marqué : sillon longitudinal fin et peu profond mais assez long, n'atteignant cependant ni la base ni le bord antérieur : dépressions basilaires en forme de petits traits linéaires longitudinaux : gouttière marginale fine, profonde sur tout son parcours : bourrelet latéral élargi dans la moitié postérieure : surface imponctuée, finement aciculée-chagrinée sur les côtés de la base : microsculpture réticulaire fine et serrée. Soie prothoracique antérieure insérée à la fin du premier tiers, la postérieure à l'angle même.

Élytres courts et larges, trapus, ovoïdes, convexes, 2,5 fois plus longs que le pronotum, 1,4 fois plus longs que larges, faiblement élargis au milieu, rétrécis régulièrement en arrière : repli basilaire entier et très droit, formant un léger denticule à l'épaule : apex légèrement acuminé : stries étroites et peu profondes, légèrement ponctuées, atteignant toutes le repli basilaire et continuées jusqu'à l'apex où elles ne sont pas plus profondes : striole scutellaire peu marquée : intervalles plats, imponctués, à microsculpture réticulaire isodiamétrale, le huitième bien plus étroit que les autres mais non linéaire : pas de fouet basilaire ni de pores dosraux. Série ombiliquée du type normal : 6 fouets huméraux, 9 fouets postérieurs (4+5), les deux groupes largement séparés.

Dessous glabre et imponctué. Prosternum légèrement sillonné longitudinalement chez le ♂. Apophyse prosternale non rebordée, sans soies, élargie et arrondie à l'extrémité. Métépisternes un peu allongés et nettement rétrécis en arrière. Épipleures élargis en avant. Soies abdominales présentes : 2 soies anales chez le ♂, 4 chez la ♀. Pattes courtes : protarses dilatés chez le ♂ et munis de deux rangées de grandes phanères adhésives : éperon interne des protibias simple ; mésotibias arqués ; métatibias des ♂♂ avec une brosse de poils courts étendue sur la moitié distale de la face interne.

Organe copulateur très arqué ; style droit avec un harpon terminal bien marqué (fig. 6).



TEXT-FIG. 6.

Amara fairmairei Raffray, édage ($\times 15$).

Par l'apophyse prosternale glabre et non rebordée, par le style droit de l'organe copulateur terminé par un crochet en forme de harpon et par la forme ramassée et trapue, cette espèce n'est pas une *Amara* proprement dite mais se rapproche du genre paléarctique *Acorius* Zimmermann, tout en ne pouvant y rentrer par suite des métatibias du ♂ muni d'une brosse de poils. Je préfère cependant la laisser dans le genre *Amara* s.l. tant qu'une révision générale des genres et sous-genres des Zabrinæ mondiaux n'ait été effectuée.

SIMIEN : Lori, c. 11,500 ft., 27-29. xi. 1952, from plateau near church of Kidana Mihar, 2 ex. ; Arghine, 11,500 ft. (or higher), 24. xi. 1952, 6 ex., collected near torrent in ravine ; Mai Datcha (E. of Arcuasié), c. 13,200 ft., 5. xiii. 1952, from slopes of marshy valley, 1 ex.—Nombre total d'exemplaires : 9.

Amara africana Putzeys.

Amara africana Putzeys, *Ann. Soc. ent. Belg.* **15**, 99, 1872 ; Alluaud, *Voyage Baron Maurice de Rothschild en Éthiopie* 1904-5, p. 505, 1922 ; Basilewsky, *J. Linn. Soc. (Zool.)*, **42**, p. 280, 1953.

Amara abyssinica Raffray, *Ann. Soc. ent. Fr.* (6) **5**, p. 317, 1885 ; Alluaud, *Voyage Baron Maurice de Rothschild en Éthiopie* 1904-5, p. 505, 1922 ; *id.*, *Ann. Mag. nat. Hist.* (10), **19**, p. 274, 1937 ; G. Müller, *Coleop. Miss. Biol. Paese Borana*, **2**, p. 20, 1940 ; Straneo, *Mem. Soc. ent. Ital.* **22**, p. 92, 1943.

(?) *Amara aethiopica* Tschitschérine, *Hor. Soc. ent. Ross.* **32**, p. 321, 1898.

SIMIEN : Derasghié, c. 9,800 ft., 22. xii. 1952, from grove of tall juniper-trees north of town, 2 ex.

Espèce largement répandue en Abyssinie, au-dessus de 2,000 mètres d'altitude.

Subfam. HARPALINÆ.

Gen. HARPALUS Latreille.

Les quatre espèces de ce genre citées ci-dessous sont assez largement répandues en Éthiopie, le plus souvent à des altitudes moyennes et élevées.

Harpalus frater Chaudoir.

Harpalus frater Chaudoir, *Rev. Mag. Zool.* (3) **4**, 343, 1876 ; Basilewsky, *Mém. Mus. Hist. nat. Paris*, **20**, p. 203, 1948 ; *id.*, *Ann. Mus. Congo Belge*, 8 (Zool.), **9**, pp. 13, 26, fig. 10, 1951.

SIMIEN : Derasghié, c. 9,800 ft., 22. xii. 1952, from grove of tall juniper-trees north of town, 4 ex. ; Arghine, c. 11,500 ft. (or higher), 24. xi. 1952, under stones near torrent in ravine ; Mai Datcha (E. of Arcuasié), c. 13,200 ft., 5. xii. 1952, from slopes of marshy valley, 1 ex.—Nombre total d'exemplaires : 8.

Harpalus cognatus Chaudoir.

Harpalus cognatus Chaudoir, *op. cit.*, p. 342, 1876 ; Basilewsky, *op. cit.*, p. 13, fig. 9, 1951.

SIMIEN : near Mindigabsa, c. 10,000 ft., 17. xi. 1952, 2 ex.

Harpalus agnatus Reiche.

Harpalus agnatus Reiche, in Ferret et Galinier, *Voyage en Abyssinie*, **3**, p. 275, (1847) 1850 ; Chaudoir, *op. cit.*, p. 342, 1876 ; Alluaud, *Ann. Mag. nat. Hist.* (10) **19**, p. 284, 1937 ; Straneo, *Mem. Soc. ent. Ital.* **22**, p. 95, 1943 ; Basilewsky, *op. cit.*, pp. 13, 27, fig. 6, 1951.

Harpalus asphaltinus Roth, *Arch. Naturg.* **17** (1), p. 117, 1851.

Harpalus germanus Chaudoir, *op. cit.*, p. 343, 1876.

SIMIEN : ravine on W. side of Mai Shaha valley, c. 9,000 ft., 14. xii. 1952, 1 ex. ; between Shaha Ghiyorghis and Derasghié, 9,300-9,800 ft., 18-20. xii. 1952, 3 ex. ; Derasghié, c. 9,800 ft., 22. xii. 1952, from grove of tall juniper-trees north of town, 6 ex. ; Mecana torrent, below Mecana-Abbo, c. 10,000 ft., 9. xii. 1952, 1 ex. ; Mai Datcha (E. of Arcuasié), c. 13,200 ft., 5. xii. 1952, from slopes of marshy valley, 1 ex.—Nombre total d'exemplaires : 12.

Harpalus impressus Roth.

Harpalus impressus Roth, *op. cit.*, p. 117, 1851; Chaudoir, *op. cit.*, p. 342, 1876; Alluaud, *l.c.*, 1937; G. Müller, *Miss. Biol. Paese Boruna*, 2 (1), p. 35, 1940; Straneo, *op. cit.*, p. 96, 1943; Britton, *Brit. Mus. (Nat. Hist.) Exp. S.W. Arabia* 1937-8, 1 (10), p. 110, 1949; Basilewsky, *Rev. fr. Ent.* 13, p. 183, figs. 20, 25, 1946; *id.*, *Ann. Mus. Congo Belg.*, 8° (Zool.), 9, pp. 12, 19, fig. 2, 1951; *id.*, *J. Linn Soc. (Zool.)*, 42, p. 287, 1953.

Harpalus hamasiensis G. Müller, *Atti Mus. Civ. Stor. Nat. Trieste*, 16, p. 81, 1947.

SIMIEN : ravine on W. side of Mai Shaha valley, c. 9,000 ft., 14. xii. 1952, 1 ex.

Subfam. CHLAENIINAE.

Chlaenius dinodoides Chaudoir.

Chlaenius dinodoides Chaudoir, *Rev. Mag. Zool.*, (3) 4, p. 359, 1876; *id.*, *Ann. Mus. Civ. Stor. Nat. Genova*, 8, p. 81, 1876.

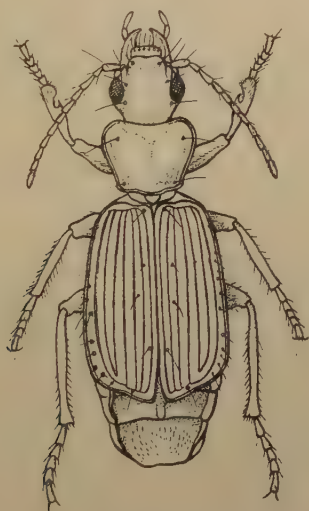
SIMIEN : near Enchetcab, over 9,000 ft., 25. xii. 1952, 1 ex. ; Arghine, 11,500 ft., 24. xi. 1952, 6 ex. collected in the ravine (three of them taken under stones near the torrent).—Nombre total d'exemplaires : 7.

Espèce décrite d'Adoua par Chaudoir et citée par le même auteur des bords du lac Tsana (Tana), d'après des récoltes de Raffray.* Je ne connaissais que le type, actuellement au Muséum de Paris.

Subfam. LEBIINAE.

Afrotarus raffrayi (Fairmaire). (Fig. 7.)

Cymindis raffrayi Fairmaire, *Le Natur.*, III, n° 24, p. 191, 1882; *id.*, *Ann. Soc. ent. Fr.*, (6) II, p. 89, 1883; Alluaud, *Ann. Soc. ent. Fr.* 86, p. 105, 1917.



TEXT-FIG. 7.

Afrotarus raffrayi Fairmaire ($\times c. 8$).

SIMIEN : Derasghié, c. 9,800 ft., 22. xii. 1952, from grove of tall juniper-trees north of town, 2 ex.

* Adua lies at about 6,200 feet, and Lake Tana at about 6,000 feet; *Chlaenius dinodoides* therefore appears to occur through at least 5,500 feet of altitude, as well as being widely distributed in northern Ethiopia.—H, S,

Décrit par Fairmaire d'une montagne d'Abyssinie, sans précision, à 4,300 mètres (c. 14,100 ft.). Alluaud la cite de la zone alpine des montagnes du Lasta,† probablement d'après Fairmaire, car je ne connais aucune autre capture de cette espèce.

Le genre *Afrotarus* a été créé récemment par Jeannel pour les espèces africaines classées comme *Cymindis*: *raffrayi* Fairmaire, d'Abyssinie, *kilimanus* Kolbe (= *kolbei* Alluaud) et *alluaudi* Jeannel, du Kilimandjaro. Il faut y ajouter *scotti* Basilevsky, de l'Arabie du Sud-Ouest (Yemen, 1938 : Jebel Sumara, c. 9,200 pieds : Jebel Jalal, entre 9,600 et 10,000 pieds).

[*Philorhizus* sp.]

TACAZZÉ RIVER: from south slope of valley, between 3,000 and 5,000 ft., 24. i. 1953, 1 ex. from soil at roots of the bamboo *Oxytenanthera abyssinica* (A. Rich.) Munro.

Though the species could not be determined from a single specimen, this record is included, to indicate the occurrence of a *Philorhizus* at the place, and in the habitat, named.—H. S.]

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† The locality where *Afrotarus raffrayi* was originally discovered has been termed "Mont Lasta". I do not know if any particular mountain is so called, but Raffray himself wrote of "les sommets du Lasta", indicating the peaks of the crest of which Abuna-Yosef on the west, and Abbi Miéda on the east, are the culminating points (Note sur la dispersion géographique des Coléoptères en Abyssinie; *Ann. Soc. ent. Fr.* (6) 5, 299, 300, 1885). The Lasta mountains lie about 100 miles south-east of Simien, on the opposite side of the Tacazzé valley.—H. S.

AN INTRODUCTION TO THE BRITISH MESOSTIGMATA (ACARINA) WITH
KEYS TO FAMILIES AND GENERA. By G. OWEN EVANS, Department of
Zoology, British Museum (Nat. Hist.).

(With 92 text-figures.)

[Read 6 October 1955.]

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INTRODUCTION.

The Acarina or mites are amongst the most numerous of the terrestrial arthropods. The majority are free-living and reach their maximum numbers in the upper layers of the soil whilst others have become adapted to a parasitic mode of life and show considerable modification in the structure of the mouthparts and respiratory organs. Although mites occur in abundance in a variety of habitats, our knowledge of the systematics of the group is still fragmentary, especially outside the Palaearctic region. This is probably due to their small size which necessitates special techniques for studying them under the compound microscope, and to the fact that their economic importance—a factor which often stimulates fundamental systematic work on a group of animals—has largely been overshadowed by that of the Insecta. The object of the present work on the suborder Mesostigmata is two-fold, namely, to provide the non-specialist with an introduction to the group and to stimulate more detailed investigations on the British fauna.

Our present knowledge of the British Mesostigmata is essentially based on the pioneer work of A. D. Michael, J. N. Halbert and J. E. Hull. Although Michael's work is chiefly associated with the excellent monographs on the Oribatidae and Tyroglyphidae he produced for the Ray Society during 1884 to 1903, his contributions to the study of the anatomy and external morphology of the Mesostigmata are not less important. Halbert (1915, 1920 & 1923) in his investigations on the Irish fauna, particularly the acarine fauna of the intertidal zone, added a large number of species to the British list. Hull (1918 & 1925) concentrated on the fauna of north-east England and his key work on the British 'Gamasiidae' published in 1918 is the only comprehensive monograph on this part of our fauna. Unfortunately some of his descriptions and figures of new species are inadequate for their certain recognition. Recently, Turk (1953) has produced "A synonymic catalogue of the British Acari" in which he lists about 360 species of mesostigmatid mites. This is an invaluable guide to the species represented in the British fauna and should be consulted in any detailed investigations on the group.

TECHNIQUES.

Collecting. Owing to the small size of the majority of free-living mites special techniques are required for collecting them in any quantity. The most satisfactory and certainly the simplest method is that described by Berlese (1905 a), whereby mites and other arthropods susceptible to dessication are driven out of samples of litter or humus by heat. Several modifications of the apparatus devised by Berlese have been developed subsequently. A simplified Berlese Funnel is described in detail in *Instructions for Collectors* No. 9 a, Brit. Mus. (Nat. Hist.), 1954, Ed. 2.

Preserving. Terrestrial mites should be preserved in 70 to 80% alcohol (industrial spirit) to which glycerine (up to 5%) may be added to prevent the specimens drying out through the evaporation of the alcohol during storage. Dried out specimens may be recovered by gently warming them in 60% lactic acid.

Preparation for study. The preparation of mites for study under the compound microscope involves the removal of their internal organs in order that other structures of taxonomic importance can be examined. The following techniques are based on those described by Evans & Browning (1955).

All developmental stages of mesostigmatid mites can be cleared by immersion in cold or warm 50 to 100% lactic acid; the strength of the lactic acid depending on the degree of sclerotization of the specimen, e.g. the lower concentrations for immature stages and other weakly sclerotized forms and the higher concentrations for heavily sclerotized species. Clearing in cold lactic acid which is preferable, may take from 3 to 5 days.

The next stage in the preparation of the mite is its orientation in a fluid medium. This can take the form of a temporary or a permanent preparation.

Temporary preparation. The specimen is transferred, together with a small quantity of the clearing fluid, to a microscope slide, orientated and a cover-slip applied. The specimen is now ready for examination. An alternative method is to transfer the specimen directly from the preservative to a drop of lactic acid on a slide, orientate, apply the cover-slip, and clear by gently warming the slide on a hotplate.

For more critical study, a perspex cavity cell can be used for containing the specimen during orientation (see Evans & Browning, 1955).

The chief advantages of the temporary methods are the speed with which the specimen can be prepared for study and the ease with which it can be orientated.

Permanent preparation. Permanent preparations are usually made in gum-chloral or polyvinyl alcohol (PVA) media. Neither of these is entirely satisfactory since the specimen deteriorates through overclearing or distortion within a relatively short time of mounting. Permanent preparations are useful, however, for building up a 'type' collection for comparative purposes. The writer has found Faure's medium* to be fairly satisfactory for this purpose. The specimen can be transferred directly from the preservative or from the clearing fluid, into the mountant. It is advisable to seal the cover-slip within about a week of preparing the mount.

All specimens, whether stored in alcohol or mounted on slides, should be fully labelled with details of habitat, locality and date of collecting.

CLASSIFICATION OF THE MESOSTIGMATA.

Grandjean (1935) has proposed the division of the Acarina into two groups, the Actinochitinosi and the Anactinochitinosi, on the characteristics of certain setae of the legs when examined with polarized light. In the former these setae have a core or axis of special chitin (active chitin) which results in their being birefringent whereas in the latter the chitin is inactive and the setae lack this

* Faure's medium contains: Distilled water, 50 c.c.; Chloral hydrate, 50 gm.; Glycerine, 30 c.c.; Gum arabic or acacia, 30 gm. The ingredients are mixed in that order at room temperature. It may be necessary to filter the medium through bolting silk before use.

property. The Actinochitinosi comprises the suborders Prostigmata and Cryptostigmata, and the Anaetinochitinosi the Mesostigmata and Metastigmata.

The Mesostigmata may be readily separated from the other suborders of mites encountered in the British fauna by the characters given in the following key :

- | | |
|---|--|
| 1. Terminal segment (tarsus) of the pedipalp with a forked seta ventrally on its inner basal angle ; stigmata, one on each side of the body, situated ventro- or dorso-laterally in the region of coxae II to IV and usually provided with an elongate peritreme ; chelicerae usually chelate but may be modified in parasitic species | MESOSTIGMATA (PARASITIFORMES). |
| - Terminal segment of the pedipalp without a forked seta ; stigmata with or without peritremes | 2. |
| 2. Hypostome modified into a harpoon-like structure provided with numerous recurved teeth ; stigmata, one on each side of the body, situated anterior or posterior to coxae IV. Ectoparasites of vertebrates..... | METASTIGMATA (IXODIDES). |
| - Hypostome not modified into a harpoon-like structure ; stigmata situated on various parts of the body or absent ; with or without pseudostigmatic organs | 3. |
| 3. Tracheal system opening through stigmata or ' pores ' on various parts of the body, or absent ; chelicerae chelate, rarely modified ; pedipalps simple ; tibia I and II usually with a long whip-like seta dorsally ; apodemes (subcutaneous sclerotized ridges, associated with the coxae of the legs, for attachment of muscles) usually well-developed. Body weakly or strongly sclerotized | CRYPTOSTIGMATA |
| - Tracheal system opening by a pair of stigmata situated on or near the gnathosoma, or absent ; chelicerae and pedipalps usually strongly modified ; tibia I and II usually without long whip-like setae dorsally. Body usually poorly sclerotized | (SARCOPTIFORMES).
PROSTIGMATA (TROMBIDIFORMES). |

The present classification of the higher groups of the Mesostigmata i.e. those divisions above family rank. is based on the late Dr. I. Trägårdh's fundamental work on the comparative morphology of the sternal and genital shields in the females of the suborder*. The results of this work are summarized by Trägårdh (1946).

Two basic types of ' genital ' shields, the parasitid-type and the fedrizsid-type occur in the females of this suborder, at least in British species. In the former the genital orifice is covered by a single shield, the genital, whereas in the latter there are three genital covers, namely, the genital and the paired lateral shields. The genital shield in the parasitid-type is frequently fused with part of the ventral shield. The three ' genital ' shields in the fedrizsid-type show considerable variation in form either through the reduction in size of one or more shields or through their coalescence. Whether these basic types represent two distinct lines of evolution within the Mesostigmata or whether the fedrizsid-type has evolved from the parasitid-type by the elaboration of the genital or vaginal sclerites is not yet decided.

Although the researches of Trägårdh have added greatly to our knowledge of the Mesostigmata the classification of the higher groups is still unsatisfactory. There has been a general tendency amongst acarologists to concentrate on the higher groupings without sufficient regard for the fundamental unit of the classification, the species. It seems desirable at present, to build up our knowledge of the world fauna, particularly the free-living species of the tropical regions which have been little studied, before attempting to revise the existing classification. The divisions or cohorts in current use may be regarded, provisionally, as convenient superfamily groupings. Bearing this in mind, the British mesostigmatid mites may be divided into the following major groups.

* Since the completion of the manuscript of this paper, CAMIN, J. & GORRIROSSI, F. (1955) [*Chic. Acad. Sci. Special. publ.* 11: 1-70] have revised Trägårdh's classification of the higher groups of the Mesostigmata.

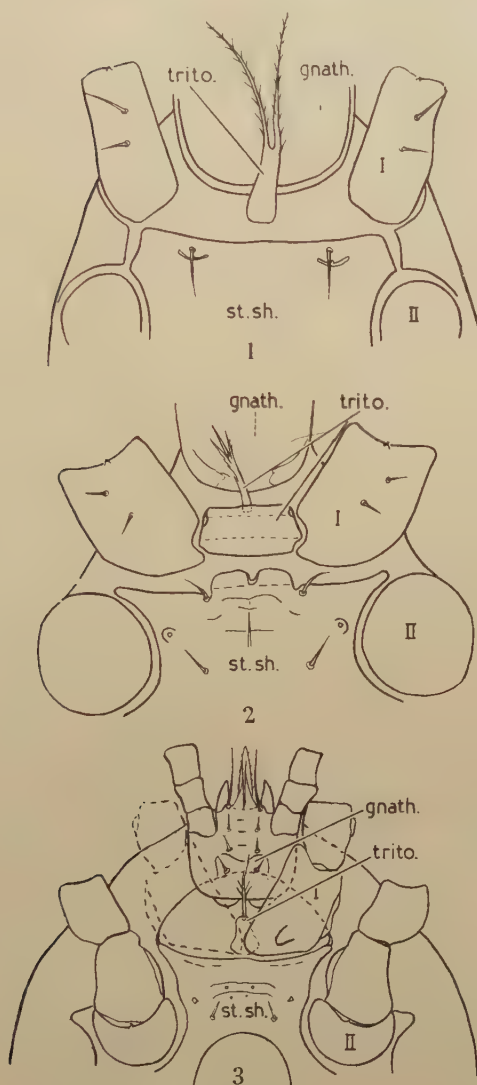
1. Tritosternum with a narrow base and usually a pair of lacinae (except in some specialized parasitic species where it is rudimentary i.e. without lacinae, or absent) and widely removed from coxae I (fig. 1) 2.
- Tritosternum otherwise, lying close to or covered by coxae I (figs. 2 & 3) 7
2. Genital orifice of the female covered by a single shield which may be fused with the ventral shield (figs. 3 & 34); digits of the chelicerae in the female without branched processes; movable digit of the male chelicera with or without a spermatophoral process 3.
- Genital orifice of the female covered by three shields, the genital and the paired laterals, which may be free (fig. 91) or coalesced (fig. 92); one or both digits of the chelicera in both sexes with branched processes; male without spermatophoral process. Represented in Britain by *Celaenopsis* Berlese and *Antennophorus* Haller, only .. FEDRIZZOIDEA.
3. With praesternal setae; stigmata and well-developed peritremes mainly dorsal in position; jugularia large extending to the middle of coxae II; genital shield tongue-shape fused posteriorly with the ventral shield; dorsal shields characteristic in form (fig. 62). Only one British species, *Thinozercon michaeli* Halbert..... THINOZERCONOIDEA.
- Without praesternal setae; peritreme lateral, if dorsal then markedly reduced in length 4.
4. Female with a large genital shield reaching to the middle of coxae II (fig. 65); sternal setae III and IV situated in the region of coxae II; genital orifice of the male near the anterior margin of the sterni-genital shield; body characteristically shaped. One British species, *Liroaspis togatus* (C. L. Koch) LIROASPOIDEA.
- Female without a large genital shield reaching to coxae II; sternal setae IV situated between coxae III or III and IV..... 5.
5. Genital orifice of the female surrounded by a sclerotized shield and covered by a large genital shield bearing one pair of setae (fig. 70); dorsal shield separated from the vertex shield; gnathosomal setae arranged as in fig. 67 PROTODINYCHOIDEA.
- Genital shield not enclosed in a sclerotized shield; genital shield with one or more pairs of setae; gnathosomal setae arranged as in fig. 11 6.
6. Genital orifice of the male at or near the anterior margin of the sterni-genital shield (fig. 29); movable digit of the male chelicera with a spermatophoral process except in some specialized parasitic species PARASITOIDEA.
- Genital orifice of the male situated in the region of coxae III and covered by two shields (fig. 55); movable digit of the chelicera in the male without a spermatophoral process. The females of this group can be distinguished from those of the Parasitoidea by the characteristic ornamentation* and structure of the dorsal shield or shields EPICRIOIDEA.
7. Tritosternum with a short broad base lying close to but never covered by coxae I (fig. 2); gnathosomal setae arranged as in fig. 74; without grooves or depressions for the legs; dorsal shield reticulated etc., often with adherent nymphal skins TRACHYTOIDEA.
- Tritosternum with a narrow base and partly or completely covered by coxae I (fig. 3); gnathosomal setae arranged as in the Trachytoidea; with or without depressions for the legs; dorsal shield smooth or ornamented but without adherent nymphal skins UROPODOIDEA.

MESOSTIGMATA-PARASITOIDEA.

This division contains over 65 per cent of the species of mesostigmatid mites recorded from the British Isles. It comprises free-living as well as specialized ecto- and endo-parasitic species. The former reach their maximum abundance in litter under deciduous and coniferous trees, in humus and in the upper layers of the soil. The specialized forms parasitize both warm and cold blooded animals.

In all post-embryonic stages the body is divided into two well-defined regions: a tubular *gnathosoma* attached antero-ventrally to a larger sac-like *idiosoma* (fig. 4). The gnathosoma is formed by the appendages of the first and second segments, namely, the *chelicerae* and *pedipalps*.

* The genus *Epicriopsis* Berlese (*Parasitoidea-Neoparasitidae*) has similar tubercles to *Epicrius* Can. & Fan. on the dorsal shield but they do not form a polygonal network!



FIGS. 1-3.—Structure of the tristosternum and coxae I in the PARASITOIDEA (fig. 1), TRACHYTOIDEA (fig. 2), and UROPODOIDEA (fig. 3).
gnath., gnathosoma ; st.sh., sternal shield ; trito., tritosternum ; I, II, coxae I & II.

The Gnathosoma : The chelicerae, the only pre-oral appendages in the Arachnida, are three-segmented in the Parasitoidea. The shaft consists of a short basal segment to which a strong retractor muscle is attached, and a larger distal segment terminating in a *fixed digit* (*f.f.*) The third segment, the *movable digit* (*m.f.*) is situated ventrolaterally to the distal segment (fig. 5). In the non-specialized, free-living species which form the greater part of the group, the chelicerae are *chelate* with the opposing edges of the digits provided with distinct teeth (figs. 5-7). The exterior face of the fixed digit bears a *dorsal seta* (*d.s.*), a *dorsal 'pore'* (*d.p.*), a large *lyriform pore* (*lyr.p.*) and one or more *ventral setae* (*v.s.*). The fixed digit may also be provided with a specialized seta, the *pilus dentilis* or *dentarius* (*p.d.*). This seta shows considerable

variation in size and shape in closely related groups of species. In the male, the movable digit carries a conspicuous structure termed the *spermatophoral process* (*sp. p.*). This process arises from the proximal half of the digit and may be fused distally with the digit as in *Pergamasus* (fig. 6) or free as in *Macrocheles* (fig. 7). The spermatophoral process functions as an accessory copulatory organ and is present only in those groups in which the male genital orifice is situated anterior to the middle of coxae II. Both digits of the chelicera show considerable modification in structure in the 'parasitic' forms. The digits may be devoid of teeth (fig. 8), e.g. *Ornithonyssus* and *Laelapsis*, the movable digit may be markedly reduced in length, e.g. *Blattisocius* and *Rhinoecius*, or both digits developed into stylet-like organs for piercing the skin of the host as in *Dermanyssus* (fig. 9).

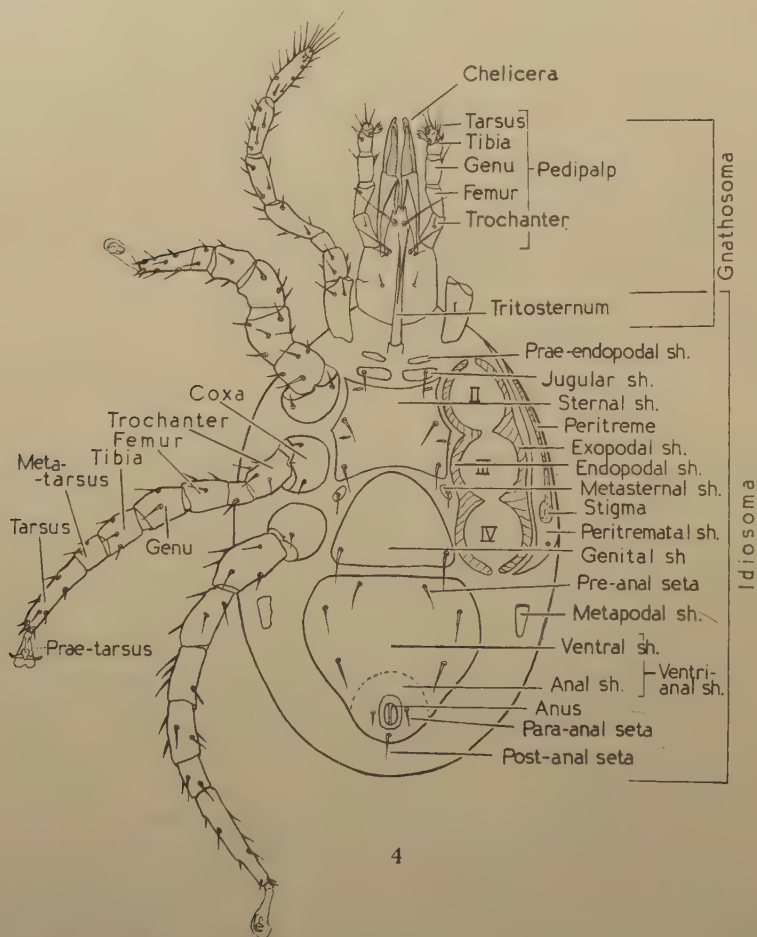
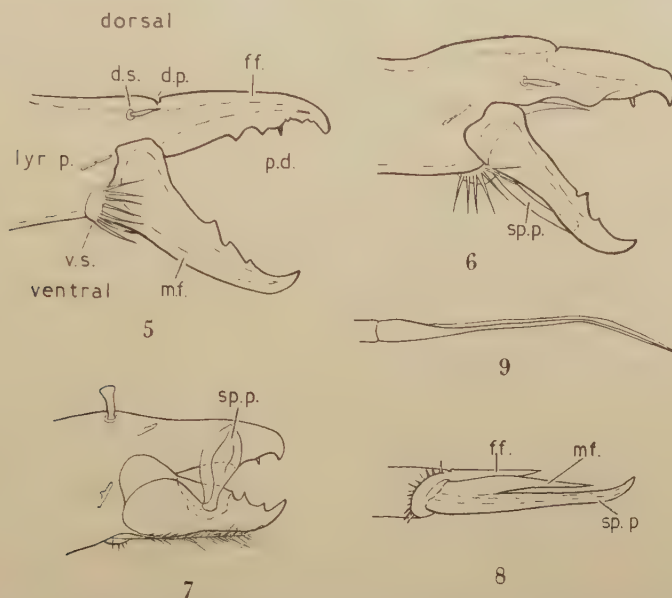


FIG. 4.—Structure of the venter of a parasitoid mite (diagrammatic).

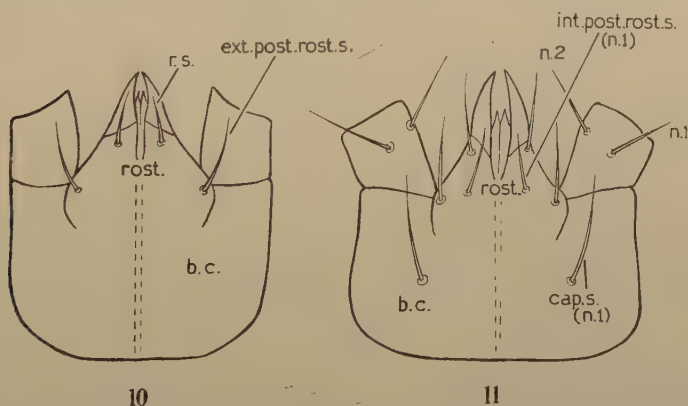
The major part of the gnathosoma consists of the *basis capituli* (*b.c.*) which forms a sclerotized tube enclosing the chelicerae (figs. 10 and 11). The dorsal wall of this tube is formed by the basal region of the *tectum* (*tect.*)—the *epistome* of some authors. The *tectum* is produced anteriorly to roof the *rostrum* (*rost.*) (fig. 12). Its anterior margin may be smooth, denticulate (fig. 13) or developed into simple or complex processes (figs. 14–17, 36). The lateral and ventro-lateral walls of the *basis capituli*

are formed by the *coxae* of the *pedipalps* which are separated ventrally by the *hypostome*. The latter bears a *ventral or capitular groove (v. gr.)* provided with rows of denticles. The *capitular setae (c.s.)* are situated on either side of the groove



FIGS. 5-9.—Form of the chelicerae in some PARASITOIDEA. Fig. 5, *Pergamasus* sp. ♀; Fig. 6, *Pergamasus* sp. ♂; Fig. 7, *Macrocheles* sp. ♂; Fig. 8, *Haemolaelaps casalis* (Berl.) ♂; Fig. 9, *Dermanyssus gallinae* (Degeer) ♀.

d.p., dorsal pore; d.s., dorsal seta; ff., fixed finger; lyr.p., lyriform organ; m.f., movable digit; p.d., *pilus dentilis*; sp.p., spermatophoral process; v.s., ventral setae.



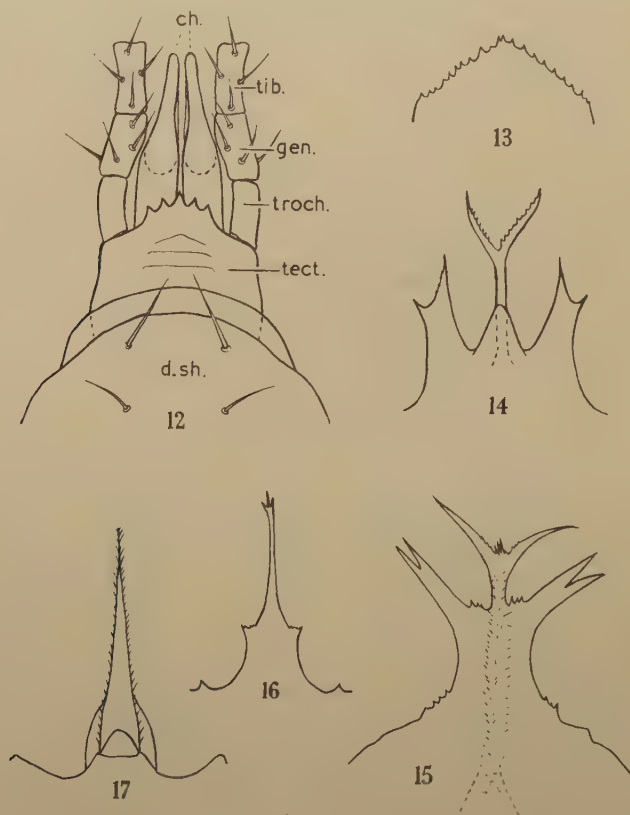
FIGS. 10-11.—Ventral view of the gnathosoma in a larva (fig. 10) and female (fig. 11) of a phytoseiid mite.

b.c., *basis capituli*; cap.s., capitular seta; n1, n2, protonymphal and deutonymphal setae, respectively; post.rost.s., internal (int.) and external (ext.) posterior rostral setae; rost., rostrum; r.s., rostral seta.

(fig. 11). Anteriorly the basis capituli carries the rostrum and the free segments of the pedipalp. The rostrum, in the nymphal and adult stages bears three pairs of setae; the *rostrals (r.s.)* and the paired *interior and posterior rostrals (int. & post.*

rost. s.). The most conspicuous structures associated with the rostrum are the *corniculi* (*corn.*) and the *internal malae* (*int. mal.*). For a more detailed account of the structure of the rostrum the reader is referred to Hughes (1949).

The five free segments of the pedipalps are attached by the *trochanter* (*troch.*) to the antero-lateral angles of the *basis capituli* (fig. 12). The palps are freely movable. Each of the five segments, namely, *trochanter*, *femur* (*fem.*), *genu* (*gen.*), *tibia* (*tib.*) and *tarsus* (*tar.*), is provided, at least in the nymphal and adult stages, with a number of setae (figs. 18 & 19). The chaetotaxy of the trochanter, femur and genu is a valuable taxonomic character and these three segments in the adults of non-specialized

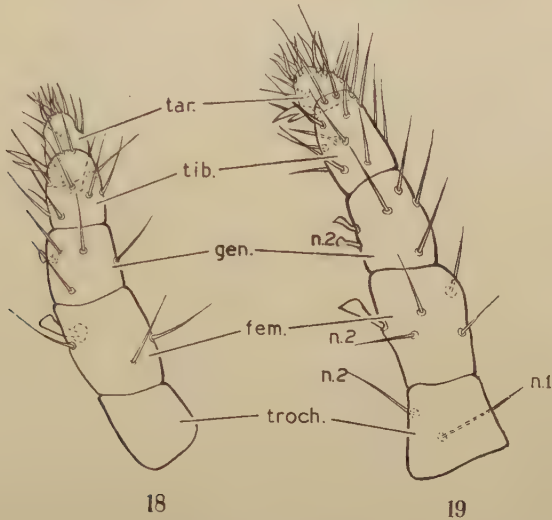


FIGS. 12-17.— Structure of the tectum (epistome).* Fig. 12, *Pergamasus crassipes* (L.) ♀; Fig. 13, *Hypoaspis* sp. ♀; Fig. 14, *Veigaia transisalae* (Ouds.) ♀; Fig. 15, *Macrocheles tridentinus* (G. & R. Can.) ♀; Fig. 16, *Geholaspis* (G.) *longispinosus* (Kr.) ♀; Fig. 17, *Eriphis ostrinus* (Koch) ♀.

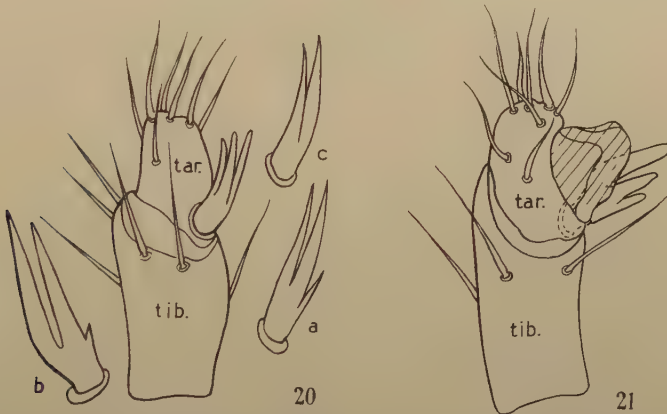
species usually bear, respectively, two, five and six setae (fig. 19). The post-embryonic development of the chaetotaxy of the palp is considered in more detail below (p. 214). In all but a few endo-parasitic species the palptarsus carries ventrally on its internal basal angle a conspicuous pronged seta (fig. 19). The number of prongs in a given species appears to be constant during post-embryonic development and is regarded as a valuable taxonomic character. The seta may be two, three or four pronged with the prongs subequal or markedly different in length (figs. 20 *a*, *b*, *c* & *d*). In the family Veigaiaidae a large leaf-like structure ('blattformige' structure) is associated with the seta (fig. 21).

* Correction to Fig. 12: for 'gen.' read 'fem.'; for 'tib.' read 'gen.'.

The Idiosoma. The *idiosoma*, generally round or oval in outline, shows no definite evidence of primary segmentation (fig. 4). Its dorsal surface in the adult stages is partially or completely covered by one or more sclerotized shields. A single *dorsal shield* may be entire (figs. 22 & 23) or deeply incised laterally as in *Veigaiia* (fig. 24) and *Arctoseius*. Those species with two dorsal shields may have the posterior shield



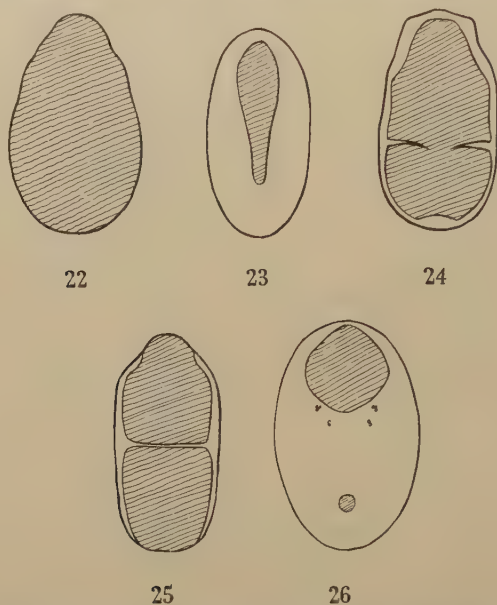
FIGS. 18-19.—Segmentation and chaetotaxy of the pedipalp in a phytoseiid mite. Fig. 18, larva; Fig. 19, female.
fem., femur; gen., genu; tar., tarsus; tib., tibia; troc., trochanter. Other abbreviations as in Fig. 11.



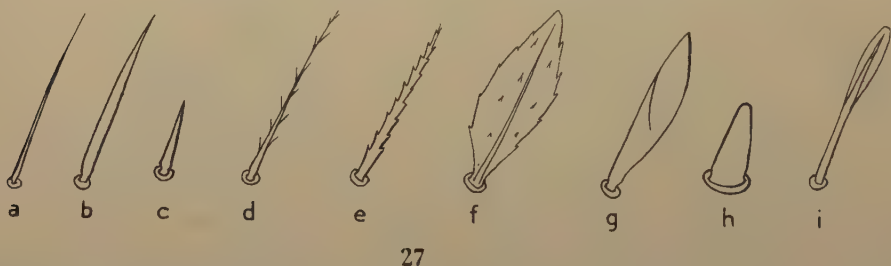
FIGS. 20-21.—Structure of the palptarsal seta in the PARASITOIDEA showing two- and three-pronged forms (Figs. 20, a-c), and the hyaline structure associated with the seta in *Veigaiia* sp. (Fig. 21). Abbreviations as in Fig. 19.

(the *notogaster*) approximately equal in size to the anterior one (the *notocephale*) as in *Digamasellus* (fig. 25) or considerably smaller than it as in *Ophionyssus* (fig. 26). In some of the endo-parasitic species the dorsum is partially covered by a number of small shields. The surface of the dorsal shield or shields may be smooth, reticulated or punctured. The lateral and posterior margins of the body in those species

in which the dorsum is incompletely covered by one or more shields is formed by a smooth, striated or granular *interscutal membrane* (figs. 37-39). The dorsal shield and often the interscutal membrane carries a number of setae. These may be simple or complex (cf. fig. 27). The chaetotaxy of the shield and membrane in some groups is of importance in separating both genera and species. This is particularly so in the Phytoseiidae and the Aceosejidae. In the former the 16 to 18 pairs of setae on the dorsal shield are divided into three longitudinal rows comprising a dorsal



FIGS. 22-26.—Types of dorsal shield or shields. Fig. 22 *Pergamasus crassipes* (L.); Fig. 23 *Ornithonyssus bacoti* (Hirst); Fig. 24, *Veigaiia transisalae* (Ouds.); Fig. 25, *Digamasellus circuliiformis* Leitner; Fig. 26, *Ophionyssus natricis* (Gervais).



FIGS. 27.—a-i, Types of setae. a, simple; b, lanceolate; c, spine-like; d, pilose; e, serrate; f, leaf-shaped; g, spatulate; h, conical spur; i, paddle-like.

(D), median (M) and a lateral (L) series (fig. 37). In the Aceosejidae, on the other-hand, use is made of the number of dorsal setae (D) and whether the marginal series (Mg), is situated on the lateral margin of the shield or on the membrane (figs. 38 & 39).

The ventral surface of the idiosoma is covered by a number of shields (fig. 4). These are usually well-defined in free-living species but may be poorly defined or even absent in endoparasitic species. Immediately posterior to the gnathosoma

and between the coxae of the first pair of legs (coxae I) lies the *tritosternum* (*trit.*), the remnant of the sternite of the third segment. In the parasitoids it usually consists of a rectangular basal portion, longer than broad, bearing distally a pair of smooth or pilose *lacinae*. These lie in the ventral groove of the gnathosoma. The tritosternum may be absent or represented only by its basal portion in parasitic species. The *sternal shield* lies posterior to the tritosternum and extends from the posterior margin of coxae I to between coxae III and IV. This shield is formed by the fusion of the coxal shields of legs I-IV with the ventral body wall and does not represent the fused sternites of the leg bearing segments i.e. segments III to VI. The four pairs of setae (*h* 1-*h* 4) associated with the sternal shield are considered to be derived from the coxal shields. Setae IV (*h* 4) are referred to as the *metasternal setae*. One or more pairs of small shields frequently occur anterior to the sternal shield; these are called the *prae-endopodal shields*. Frequently sternal setae I (*h* 1) are detached from the sternal shield and each lies on a small shield surrounded by membrane. These seta-bearing shields are the *jugular shields* or *jugularia*.

In the female, the metasternal setae may lie on the sternal shield, on the inter-scutal membrane posterior to the sternal or on small shields (*met.sh.*) free or fused with the *endopodal shields*. The size and shape of the metasternal shields varies considerably within the suborder. Usually they are small, oval or elongate but in the Parasitidae they form large rectangular shields (almost touching or completely fused in the mid-line) flanking the *genital* or *epigynial shield* (fig. 28). The three pairs of 'pores' normally associated with the sternal setae are situated between *h* 1 & *h* 2 ('pore' 1), *h* 2 & *h* 3 ('pore' 2) and *h* 3 & *h* 4 ('pore' 3). The genital orifice is situated posterior to the sternal shield and is usually in the form of a transverse slit. Posterior to it lies a distinct genital shield (*gen. sh.*) whose anterior portion may extend over the orifice and form of a kind of 'chute' along which the egg travels during oviposition. The shield may be uniformly sclerotized as in the Parasitidae or consist of a well-sclerotized basal portion and a weakly sclerotized distal portion as in the Aceosejidae. The pair of setae (genital setae, *gen.s.*) and 'pores' usually associated with the shield either lie on the shield itself or lateral to it on the inter-scutal membrane. In the Parasitidae a pair of shields, the *parasternals*, lie between the metasternal shields and the genital shield (fig. 28).

The intercoxal region in the male is occupied by a compound *sterniti-genital shield* (*st.g.sh.*) bearing five pairs of setae which are homologous with the sternal and genital setae in the female. Prae-endopodal and/or jugular shields may be present in some species. The sterniti-genital shield and the endopodal shields are distinct or fused with each other. The genital orifice in the males of the Parasitoidea is prae-sternal in position (fig. 29), with the exception of the *Rhodocarus*-group in which it is located in the sterniti-genital shield in the region of coxae II. The genital orifice may be covered by a circular disc (Trägårdh, 1946 a).

The region posterior to coxae IV in the female is partially or almost completely covered by sclerotized shields except in some parasitic species. The posterior extension of the genital shield may be slight in which case it is widely separated from an anal shield or almost reaching the anterior margin of a large ventri-anal shield (fig. 45). In some genera e.g. *Gymnolaelaps* and *Pseudoparasitus* the shield extends almost to the anal shield (fig. 47). When this 'genital' shield bears only the genital setae it is referred to as the genital shield but if additional setae are present, indicating the fusion of the genital with part of the ventral shield, it is termed the *geniti-ventral shield* (*gen.v. sh.*). The *ventral shield* lies between the posterior margin of the genital shield and the anal shield. In the British parasitoids this shield is usually fused with one or more shields e.g. in *Veigaia* it is fused with the genital, podal or peritrematal shield whereas in *Lasioseius* it is fused with the anal shield. The *anal shield*, surrounding the anus, bears three setae only except in a few parasitic species which show increased setation of both dorsal and ventral shields, e.g. *Haemogamasus*. The three setae on the anal shield are the paired *para-anals* and the *post-anal seta*.

The para-anals are normally situated on each side of the anus but in some of the Platyseinae they may be situated posterior to it. The fusion of the ventral and anal shields results in the formation of a *ventri-anal shield* which can be distinguished from an anal shield by the presence on it of one or more pairs of *pre-anal setae*, derived from the ventral shield, anterior to the anus (fig. 45). Several other small shields may occur posterior to coxae IV. The most important of these are the *metapodal shields* situated posterior to coxae IV.

In the male the sclerotization of the postero-ventral region is generally more extensive than in the female. The sterniti-genital shield may be fused with a ventri-anal shield to form a *holoventral shield* (fig. 48) or separated from a ventri-anal or anal shield. The holoventral or ventri-anal shields are sometimes fused with the dorsal shield posteriorly.

The *stigmata* (*stig.*), one pair only, in nymphal and adult stages are situated ventro-laterally in the region of coxae III and IV. Associated with each stigma, at least in free-living forms, is a long sclerotized tube-like structure, the *peritreme* (*per.*). This extends anteriorly from the stigma to beyond coxae I. In some genera e.g. *Platyseius*, it may be developed posterior to the stigma. The position of the stigma and the degree of development of the peritreme show considerable variation in the parasitic forms. Due to the enlargement of the coxae and/or the dorso-ventral compression of the body the stigmata and peritremes are located dorso-laterally or dorsally. Further the peritremes may be greatly reduced in length e.g. in the Rhinonyssinae. The stigma and peritreme are normally enclosed in a *peritrematal shield* (*per. sh.*). This shield shows various degrees of fusion with the dorsal, *exopodal* (*exp. sh.*) and ventri-anal shields (fig. 44). In some genera e.g. *Pachylaelaps* (fig. 34) and *Platyseius* the peritrematal shield is strongly developed posterior to coxae IV.

The ambulatory appendages comprise seven segments, namely, coxa, trochanter, femur, genu, tibia, tarsus and prae-tarsus. The prae-tarsus is frequently absent. Both the femur and tarsus may show evidence of secondary division into a basi-femur and telo-femur, and a meta-tarsus and tarsus, respectively. The prae-tarsus (or tarsus) normally terminates in an ambulacral apparatus comprising two *claws* and a lobate *pulvillus*. The claws may be smooth or denticulate and the distal margin of the pulvillus gently rounded or acute (figs. 42 & 43). In the majority of species legs I are tactile in function. The ambulacral apparatus is generally reduced or may even be absent, as in the Macrochelidae. Tarsus I is provided distally with numerous rod-like sensory setae (cf. fig. 57) forming a sensory field. This 'organ' is probably homologous with Haller's organ in the Metastigmata (ticks). All segments of the legs are provided with setae which are either simple or complex. Leg II and rarely leg IV in the male may be provided with stout spurs that assist in clasping the female during copulation (fig. 30). In the Parasitidae the spur-bearing segments are often crassate.

Recognition of immature stages. The parasitoids usually have four morphologically distinct post-embryonic stages in the life-cycle, namely, *larva*, *proto-nymph*, *deuto-nymph* and *male* or *female*. One or more immature stage may be suppressed in specialized parasitic forms. The larval stage is readily distinguished from successive stages by having only three pairs of ambulatory appendages (legs I-III). The nymphal stages have four pairs of legs (and in this respect resemble the adult stages) but are without a trace of genital orifice and associated structures. In the free-living species the proto- and deuto-nymph may be separated by the chaetotaxy* of the trochanter and femur of the pedipalp (Evans, 1953). The symbols *n* 1 and *n* 2 on the figures of the pedipalp (figs. 18 & 19) and the *basis capituli* and *rostrum* (figs. 10 & 11) denote that the setae are developed during the proto-nymph and deuto-nymph respectively and would therefore be absent in the preceeding developmental stage, e.g. *n* 2 on the palptrochanter would not be developed in the larva or proto-nymph.

* A spur or spine may be present on the trochanter. This is not considered in the chaetotaxy of the segments.

The following table summarizes the major differences between the stages :

TABLE 1

Developmental Stage	Number of legs	Gnathosoma		Intercoxal region	
		Chaetotaxy of the <i>basis capituli</i> and <i>rostrum</i>	Chaetotaxy of the palptrochanter and femur	Chaetotaxy and sclerotization	Genital orifice
Larva	6	With rostrals and one pair of posterior rostrals	Trochanter without setae, femur with four	Three pairs of setae with or without sternal shield	Not developed
Protonymph	8	With rostrals, two pairs of posterior rostrals, and capitular setae	Trochanter with one seta, femur with four	Four pairs of setae with or without sternal shield	ditto
Deutonymph	8	ditto	Trochanter with two setae, femur with five	Five pairs of setae and sternal shield	ditto
Female	8	ditto	ditto	Five pairs of setae, sternal shield and part of genital shield	Transverse slit posterior to sternal shield
Male	8	ditto	ditto	Five pairs of setae and sterniti-genital shield	Prae-sternal or region of coxae II

CLASSIFICATION.

Twelve families are represented in the British fauna. Of these, the family Poecilochiridae Willmann (p. 219) is based on deutonymphal and male characters only, and is not included in the key.

Key to families.

1. Specialized seta on the palptarsus in adult and immature stages with three* or four prongs (figs. 20, 20 *a* & *b* & 21) 2.
- Specialized seta on palptarsus in adult and immature stages with two prongs (fig. 20) except in some specialized parasitic species in which the seta is rudimentary or absent..... 7.
2. Metasternal shields in the female almost or completely fused in the median line, are large and flank the anterior portion of the genital shield (fig. 28); spermatophoral process on the movable digit of male chelicera fused with the digit distally (fig. 6); leg II in male spurred (fig. 30) PARASITIDAE Oudemans.
- Without large metasternal shields flanking the genital shield in the female (metasternal setae situated on the interscutal membrane, on the sternal shield or on small shields free or fused with the endopodal shields); spermatophoral process free distally (fig. 7) 3.
3. Dorsal shield, in both sexes, entire 4.
- Dorsal shield, in both sexes, incompletely divided by strong lateral incisions, or completely divided, into two shields 6.
4. Leg I in both sexes without ambulacral apparatus..... MACROCHELIDAE Vitzthum.
- Leg I in both sexes with at least well-developed claws .. 5.
5. Posterior margin of the sternal shield in the female reaching to the middle of coxae IV; with a compound peritrematal-exopodal shield flanking the geniti-ventral shield (fig. 34) PACHYLAEALAPTIDAE Berlese.

* In some genera e.g. *Ololaelaps* Berl., and *Cyrtolaelaps* Berl. one of the prongs may be reduced in size (cf. figs. 20 *a-b*) and difficult to discern if the seta is not orientated correctly.

- Posterior margin of the sternal shield in the female not extending to the middle of coxae IV ; without large peritrematal-exopodal shield flanking a geniti-ventral shield	NEOPARASITIDAE Oudemans.
6. Dorsal shield divided into two shields or with strong lateral incisions ; specialized seta on palptarsus in both sexes with a conspicuous leaf-like structure (fig. 21) ; vaginal sclerites showing varying degrees of development ; small pygidial shield or shields present ; with a strong upright seta distally on dorsal surface of tibia IV	VEIGAIAIDAE Oudemans.
- Dorsal shield completely divided ; specialized seta on palptarsus without large leaf-like structure ; without strong upright seta distally on tibia IV	RHODACARIDAE Oudemans.
7. Dorsal shield entire in both sexes with less than twenty pairs of setae (fig. 37)* ; usually no addition of setae on the dorsal shield after the protonymphal stage ; female with a truncated genital shield and a ventri-anal shield ; male with sterniti-genital shield separated from ventri-anal shield	PHYTOSEIIDAE Berlese.
- Dorsal shield, entire or divided, with more than twenty-three pairs of setae (figs. 38 & 39) except in specialized parasitic forms ; setae added to the shield (or shields) in the deuto-nymphal stage ; female with ventri-anal or anal shield	8.
8. Genital shield in the female truncated posteriorly or very slightly convex, with not more than one pair of setae and lying close to a ventri-anal shield or remote from an anal shield (fig. 45) ; tectum may be produced into a long median process ; male with sterniti-genital shield and a separate ventri-anal or anal shield (fig. 46). Chelicerae dentate, dorsal and ventral shields well sclerotized. Free-living.....	9.
- With genital or geniti-ventral shield in the female ; posterior margin of shield strongly convex (genital shield flask-shaped) or if truncated then almost touching the anal shield (fig. 47) ; male with holovertral shield or sterniti-geniti-ventral shield separate from anal shield ; tectum not produced into a long median process (fig. 48). This family contains a number of parasitic species showing reduction in sclerotization of both dorsal and ventral shields, modification of the chelicerae and often the reduction or absence of the bipartite tritosternum	LAELAPTIDAE Berlese.
9. Dorsal shield in both sexes completely divided into two shields of approximately equal size. Leg II in the male spurred	DIGAMASELLIDAE nov.
- Dorsal shield undivided in both sexes. Leg II in the male unarmed	10.
10. †Male with sterniti-genital shield and separate ventri-anal shield (fig. 46) ; female in most genera with ventri-anal shield ; when an anal shield is present then the genital shield is without setae or the species is weakly sclerotized ; tectum never produced into an elongated process	ACEOSEJIDAE Baker & Wharton.
- Male with sterniti-genital shield and separate anal shield (fig. 46) ; genital shield, except in <i>Thinoseius</i> , with a pair of setae ; female with anal shield only ; dorsal shield strongly sclerotized ; tectum often with elongate process medially (fig. 17). Body may be strongly arched and may be provided with long stout dorsal setae	EVIPHIDIDAE Berlese.

* Not more than six setae in the dorsal series (fig. 37).
† The separation of females of these two families may cause some difficulty. The following key should assist in placing them in their correct families:

1. With ventri-anal shield	ACEOSEJIDAE
- With anal shield	2.
2. Sternal shield sclerotized ; palpgenu with six setae	3.
- Sternal shield not sclerotized ; palpgenu with five setae ..	EVIPHIDIDAE
3. Tectum produced into an elongate, denticulate process ..	EVIPHIDIDAE.
- Tectum otherwise, usually difficult to discern	4.
4. Genital shield without setae	ACEOSEJIDAE.
- Genital shield with a pair of setae	5.
5. Ventral setae normal, not numerous	ACEOSEJIDAE.
- Ventral setae short, spine-like and numerous	EVIPHIDIDAE.

Family PARASITIDAE Oudemans, 1901.*

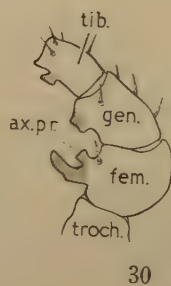
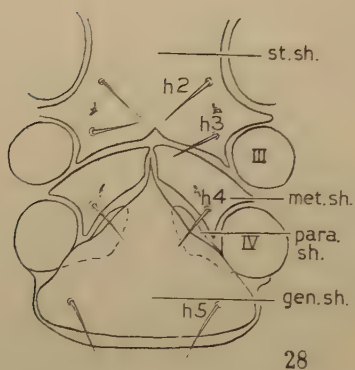
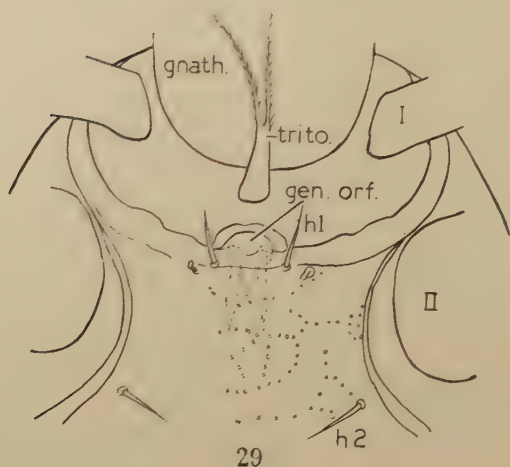
PARASITINAE Oudemans, A. C. (1901). *Tidschr. ned. dierk. Ver.* (2), 7, 59.

Representatives of this family are probably the most common and widely distributed of the parasitoids found in litter and humus. The adults, generally heavily sclerotized, are readily distinguished from other parasitoids by the structure of the genital region in the female (fig. 28) and the structure of the chelicerae in the male (fig. 6). The immature stages have a divided dorsal shield and are commonly found on beetles and other insects, which they use as a means of transportation. The deutonymph is often referred to as the *nympha coleoptrata* stage. The classification of the family is based chiefly on the excellent monograph on the genus '*Gamasus*' by Berlese (1906). Both sexes of *Parasitus* s. lat. and *Pergamasus* s. lat. are usually necessary for specific identification.

Key to genera.

1. Leg I without ambulacral apparatus; body weakly sclerotized; dorsal and ventral shields tapering posteriorly; peritreme not reaching coxae I. Small species (490 μ in length). In decaying vegetation under a birch sapling. Male unknown. *Pergamasellus* nov.
(Type: *Pergamasellus delicatus* sp. n.).
 - . Leg I with claws; dorsal and ventral shields well sclerotized 2.
 2. Metasternal shields in the female completely fused with each other; anterior margin of the genital shield rounded *Leptogamasus* Trägårdh, 1936.
(Type: *Leptogamasus suecicus* Trägårdh, 1936).
 - . Metasternal shields free or only partly fused in the median line; anterior margin of genital shield pointed 3.
 3. Dorsal shield entire, without lateral incisions, or completely divided into two shields in the adult stages; female and deutonymph without spurs on leg II. 4.
 - . Dorsal shield in the female with strong lateral incisions; female and deutonymph with stout spurs on leg II. Male unknown *Gamasodes* Oudemans, 1939.
(Type: *Gamasodes spiniger* Oudemans, 1936, nom. nov. pro *Gamasus spinipes* Koch, 1841, nec *Gamasus spinipes* Say, 1821).
 4. Dorsal shield entire in the female 5.
 - . Dorsal shield completely divided into two shields in the female *Parasitus* Latreille, s. lat.
(a) Corniculi in the male stalked (fig. 31) *Parasitus* Latreille, 1795, s. str.
(syn.: *Carpais* Latr., 1796 and *Gamasus* Latr., 1802).
(Type: *Acarus fucorum* Degeer, 1778).
 - (b) Corniculi in the male sessile (fig. 32) *Eugamasus* Berlese, 1893.
(Type: *Gamasus magnus* Kramer, 1876).
 5. Ventral shield fused with the dorsal shield posteriorly in the female *Holoparasitus* Oudemans, 1936.
(syn.: *Ologamasus* Berl., 1906, nec Berl., 1888).
(Type: *Gamasus calcaratus* C. L. Koch, 1839).
 - . Ventral shield not fused with the dorsal shield in the female *Pergamasus*, Berlese, 1904, s. lat.
- This genus has been divided into a number of subgenera (species groups!) on the armature of leg II in the male:
- (a) Genu of leg II spurred b.
 - . Without spurs on genu II *Paragamasus* Hull, 1918.
(Type: *Parasitus robustus* Oudms., 1902).
 - (b) Leg II markedly crassate; femoral spur strongly developed *Pergamasus* Berlese, s. str.
(Type: *Acarus crassipes* Linn., 1758).
 - . Leg II weakly crassate c.
 - (c) Femoral spur weak; spurs on genu and tibia retrograde *Amblygamasus* Berlese, 1904.
(Type: *Gamasus tiberinus* G. & R. Canestrini, 1882).
 - . Femoral spur conspicuous, cylindrical; spurs on genu and tibia not retrograde *Plesiogamasus* Hull, 1918.
(Type: *Pergamasus hamatus* (Koch) Berlese, 1906).

* syn. *Gamasidae* Leach, 1815.



FIGS. 28-32.—Fig. 28, structure of the sterniti-genital region in *Pergamasus* sp. Fig. 29, position of the genital orifice in *Macrocheles* sp. ♂. Fig. 30, armature of leg II in the male of *Eugamasus* sp. Fig. 31, stalked corniculus in *Parasitus* sp. ♂. Fig. 32, sessile corniculus in *Eugamasus* sp. ♂.
 ax.pr., axillary process; corn, corniculus; fem, femur; gen.orf., genital orifice; gen.sh., genital shield; gen., genu; gnath., gnathosoma; h 1-h 4, sternal setae; h 5, genital seta; met.sh., metasternal shield; para.sh., parasternal shield; st.sh., sternal shield; tib., tibia; trit., tritosternum; troch., trochanter.

Family POECILOCHIRIDAE Willmann, 1940.

POECILOCHIRIDAE Willmann, C. (1940). *Zool. Anz.* **130**, 215.

The males of the poecilochirids are characterized by having the genital orifice in a prae-sternal shield and the second pair of legs armed with spurs. The sternal shield in the deutonymph is usually provided anteriorly with a dark transverse band. The family contains only one genus, *Poecilochirus*, G. & R. Canestrini, 1882 (Type: *Poecilochirus carabi* G. & R. Can., 1882). It is possible that when the females of *Poecilochirus* have been discovered the genus will be found to be closely related to those genera now placed in the family Parasitidae. The nymphal stages of the genus have been found on a variety of beetles.

Family MACROCHELIDAE Vitzthum, 1930.

MACROCHELIDAE Vitzthum, H. G. (1930). *Zool. Jb.* **59**, 301.

The mites in this family may be distinguished from other parasitoids by the combination of the following characters: a three-pronged tarsal seta, no ambulacral apparatus on leg I, metasternal shields small and dorsal shield entire. Further, in the British species of the family the peritreme is strongly looped in the region of the stigma. The macrochelids are widely distributed in a variety of habitats, e.g. in humus, soil, decaying wood and on insects. The majority of the species have been described by Berlese (1918) and Hull (1925). Four genera of the subfamily Macrochelinae occur in Britain and these have been revised by Evans & Browning (1956).

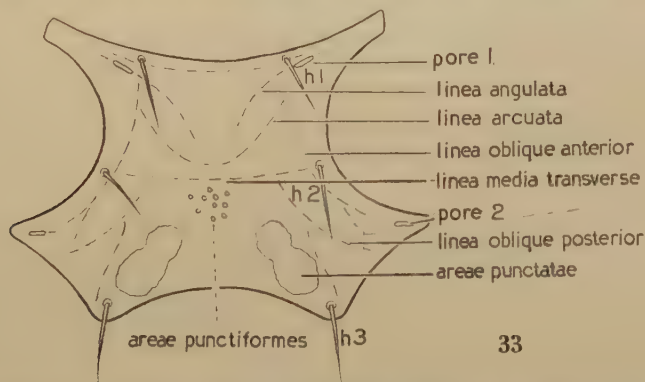


FIG. 33.—Structure and ornamentation of the sternal shield in a Macrochelid mite (based on Berlese, 1918).

Subfamily MACROCHELINAE Trägårdh, 1949.

Key to genera.

1. Femur of leg II in the female with strong spurs; vertical setae situated on an outgrowth of the dorsal shield; ventri-anal shield with four pairs of pre-anal setae . . . *Holostaspella* Berlese, 1904.
(Type: *Holostaspis* (*Holostaspella*) *sculpta* Berl., 1904).
- Femur of leg II in the female unarmed; vertical setae on the summit of the dorsal shield; ventri-anal shield with 2, 3, or 5 pairs of pre-anal setae 2.
2. Ventri-anal shield with two pairs of pre-anal setae *Macroholaspis* Oudemans, 1931.
(Type: *Gamasus opacus* C. L. Koch, 1839).
- Ventri-anal shield with three or four pairs of pre-anal setae 3.
3. Ventri-anal shield of the female with three pairs of pre-anal setae; tectum with usually three median processes (fig. 15) *Macrocheles* Latrielle, 1829.
(syn: *Coprholaspis* Berlese, 1918; *Nothrholaspis* Berlese, 1918; *Dissolonych* Falconer, 1923 and *Monoplates* Hull, 1925).
(Type: *Acarus marginatus* Hermann, 1804 = *Acarus muscaedomesticae* Scopoli, 1772).

- . Ventri-anal shield in the female with five pairs of pre-anal setae; tectum with a single median process (fig. 16) entire or divided distally..... *Geholaspis* Berlese, 1918 s. lat.
- (a) Ratio of the length of the dorsal shield to the length of the movable digit of the chelicera varies between 6·8 and 10·4. Movable digit with less than five teeth *Geholaspis* Berlese s.str.
(Type : *Gamasus longispinosus* Kramer, 1878).
- (b) Ratio of the length of the dorsal shield to the length of the movable digit of the chelicera varies between 3·7 and 4·5. Movable digit with more than five teeth *Longicheles* Valle, 1953.
(Type : *Holostaspis mandibularis* Berl., 1904).

Family NEOPARASITIDAE Oudemans, 1939*.

NEOPARASITIDAE Oudemans, A. C. (1939). *Zool. Anz.* 126, 21.

The writer has included in this family those parasitoids which have a three-pronged tarsal seta, an ambulacral apparatus on tarsus I and an entire dorsal shield in both sexes. In some of the genera included here one of the prongs of the palptarsal seta is strongly reduced in size. All the British species of the Neoparasitidae are free-living.

Key to genera.

Females.

1. Dorsal shield in both sexes richly ornamented with tubercles; dorsal setae long and stout; sternal shield with two pairs of setae in the female; anal shield broader than long. One British species (*E. horridus*) in decaying leaves, moss, etc. *Epicriopsis* Berlese, 1916.
(Type : *Gamasus horridus* Kramer, 1876).
- Dorsal shield without tubercles; sternal shield usually with three pairs of setae 2.
2. Female with ventri-anal or geniti-ventri-anal shield. 3.
- Female with anal shield 5.
3. Female with a large geniti-ventri-anal shield; dorsal shield strongly sclerotized and completely covering the dorsal and lateral surfaces of the mite; male with holovenal shield; one of the prongs of the palptarsal seta reduced in size. In moss and humus *Ololaelaps* Berlese, 1903.
(? syn. : *Hyletastea* Gistel, 1884).
(Type : *Ololaelaps venetus* Berl., 1903).
- Female with ventri-anal shield separated from truncated genital shield; specialized seta on palptarsus with prongs well-developed 4.
4. Posterior and postero-lateral margins of the ventri-anal shield in both sexes fused with the dorsal shield; tarsus II without stout spines; tectum produced into a strong triangular process. Intertidal *Hydrogamasus* Berlese, 1892.
(Type : *Gamasus littoralis* G. & R. Canestrini, 1881 - *Gamasus salinus* Laboulbene, 1851).
- Posterior and postero-lateral margins of the ventri-anal shield not fused with the dorsal shield; tarsus II with stout spines and spurs as in *Pachylaelaps*. In deciduous litter *Pachyseius* Berlese, 1910.
(Type : *Pachyseius humeralis* Berl., 1910).
5. Female with a small truncated genital shield; anal shield remote in both sexes; dorsal shield strongly sclerotized with lateral setae, at least, long and stout; one prong of palptarsal seta reduced. Under bark of trees, in humus, etc. *Ameroseius* Berlese, 1903.
(syn. : *Cornubia* Turk, 1943).
(Type : *Seius echinatus* C. L. Koch, 1839 = *Acarus corbicula* Sowerby, 1806).
- Female with a flask-shaped genital or a large geniti-ventral shield extending almost to the anal shield, male with holovenal shield; podal or peritrematal shield often well-developed posterior to coxae IV. 6.

* Including Pseudoparasitidae Vitzthum, 1941.

6. Dorsal setae simple or pilose; geniti-ventral shield almost touching anal shield; podal or peritrematal shields well-developed posterior to coxae IV; corniculi normal 7.
- Dorsal setae clavate or serrulate; anal shield remote from genital shield; podal and peritrematal shields not developed posterior to coxae IV; corniculi massive, extending almost to the distal end of the palpfemur *Stratiolaelaps* Berlese, 1916.
(Type: *Laelaps (Iphis) miles* Berl., 1882).
7. Geniti-ventral shield in the female with more than three pairs of setae; peritrematal shields free, reaching to about the middle of coxae IV; leg II in the male spurred. In humus, soil, etc. *Pseudoparasitus* Oudemans, 1902.
(syn.: *Hoplolaelaps* Berl., 1903, *Laelapsoides* Willmann, 1952).
(Type: *Laelaps meridionalis* G. & R. Canestrini, 1882).
- Genital or geniti-ventral shield in the female with less than three pairs of setae (usually only the genital setae) 8.
8. Peritrematal shield in the female free, enlarged posterior to the stigma and extending beyond the posterior margin of coxae IV. In humus *Alloparasitus* Berlese, 1920.
(Syn.: *Halbertia* Hull in Turk & S. Turk, 1952).
(Type: *Pseudoparasitus angulatus* Berl., 1920).
- Peritrematal shield in the female free but not extending posterior to coxae IV. Myrmecophilous *Gymnolaelaps* Berlese, 1916.
(Type: *Laelaps myrmecophilus* Berl., 1892).

Family RHODACARIDAE Oudemans, 1902.

RHODACARINAE Oudemans, A. C. (1902). *Tijdschr. Ent.* 45, 48.

The writer has included in this family those parasitoids with a three-pronged tarsal seta (without a 'blattförmige' structure) and with a divided dorsal shield. This concept of the family is purely practical in nature and will undoubtedly require modification when the genera included here are investigated more fully. The following seven genera are included in the British fauna.

Key to genera.

1. Body elongate with a distinct constriction behind coxae IV; anterior and posterior regions of the sternal shield weakly sclerotized and punctured; chelicerae heavily sclerotized, large and conspicuous 2.
- Body usually without a constriction behind legs IV (a weak constriction is present in some *Halolaelaps* spp.); sternal shield normal in both sexes 3.
2. Leg I without claws. Small pale species with conspicuous chelicerae. Common in soil, humus, moss, etc. *Rhodacarus* Oudemans, 1902.
(Type: *Rhodacarus roseus* Oudemans, 1902).
- Leg I with claws. Similar to preceding genus in gross morphology. Rare (?) in soil *Rhodacarellus* Willmann, 1935.
(Type: *Rhodacarellus subterraneus* Willmann, 1935).
3. Sternal shield free or incompletely fused with the endopodal shields in the female. Leg II, and sometimes III and IV armed in the male 4.
- Sternal shield completely fused with the endopodal shields in both sexes. Leg II only armed in the male 6.
4. Coxae II in both sexes with an acute or obtuse spur on its anterior margin; leg II only armed in the male 5.
- Coxae II unarmed in both sexes; legs II, III and occasionally I and IV armed in the male. Intertidal, in salt marshes or in decaying vegetation *Halolaelaps* Berlese & Trouessart, 1889.
(Type: *Halolaelaps glabriusculus* Berl. & Trouess., 1889=*Gamasus marinus* Brady, 1875).
5. Anterior margin of the posterior dorsal shield entire; female with ventri-anal shield considerably broader than long. In humus. *Leitneria* nov.
(Type: *Gamasellus (Protolaelaps) granulatus* Halbert, 1923).
- Anterior margin of the posterior dorsal shield incised; female with anal shield. In dung, compost heaps etc. .. *Saprolaelaps* Leitner, 1946.
(Type: *Saprolaelaps subtilis* Leitner, 1946).

6. Vertical setae normal; dorsal shields with simple or slightly pilose setae; tarsus I with well-developed pulvillus and claws; palptarsal setae with three distinct prongs. In nest of (and on) small mammals..... *Euryparasitus* Oudemans, 1901.
(Type: *Gamasus emarginatus* C. L. Koch, 1839).
- Vertical setae short, spinose; dorsal shields with a few stout pilose or serrated setae; tarsus I with pulvillus rudimentary or absent; one prong of palptarsal seta markedly reduced (cf. fig. 20 b). Similar in habitat to *Euryparasitus* *Cyrtolaelaps* Berlese, 1887.
(syn.: *Protolaelaps* Trägårdh, 1912).
(Type: *Gamasus macronatus* G. & R. Canestrini, 1881, syn.: *Gamasellus brevispinosus* Trägårdh, 1910 and *Asca affinis* Oudms., 1902).

Family VEIGAIIDAE Oudemans, 1939*.

VEIGAIIDAE Oudemans, A. C. (1939). *Zool. Anz.* 126, 21.

The Veigaiidae are characterized in the adult stages by the presence of a well-defined leaf-like hyaline structure associated with the specialized setae on the palptarsus (fig. 21). Three genera are represented in the British fauna. The genus *Veigaia* Oudms. is widely distributed and common in humus, soil, moss, etc. and has recently been revised by Evans (1955 c). *Cyrthyrolaelaps* Berl., on the other hand, is restricted in its distribution to the intertidal zone. The third genus, *Gamasolaelaps* Berl., occurs in wet habitats and is represented in our fauna by the genotype, *Gamasolaelaps excisus* (L. Koch).

Key to genera.

1. Specialized setae on the palptarsus in both sexes with four prongs; ventral shield well-developed in the female and remote from the anal shield; dorsal shield completely divided into two shields..... *Gamasolaelaps* Berlese, 1903.
(syn.: *Metaparasitus* Oudms. & Voigts, 1904).
Type: *Cyrtolaelaps aurantiacus* Berl., 1903 = *Metaparasitus suboles* Oudms. & Voigts, 1904 = *Sejus excisus* L. Koch, 1879).
- Specialized seta on palptarsus with three prongs; ventral shield well-developed; dorsal shield completely or incompletely divided by lateral incisions into two shields..
2. Metasternal shields fused with the endopodal shields and may or may not be connected by them to the sternal shield; ventral shield showing various degrees of fusion with the genital, podal and peritrematal shields; anal shield fused with the ventral shield in the male..... *Veigaia* Oudemans, 1905.
(syn.: *Cyrtolaelaps* Berl., 1892 nec Berl., 1887).
(Type: *Gamasus nemorensis* C. L. Koch, 1836).
- Metasternal setae situated on the sternal shield or on the interseutal membrane posterior to it; dorsal shield completely divided; with a separate anal shield in the male *Cyrthyrolaelaps* Berlese, 1904.
(Type: *Cyrthyrolaelaps hirtus* Berl., 1904).

Family PACHYLAELAPTIDAE Berlese, 1913.

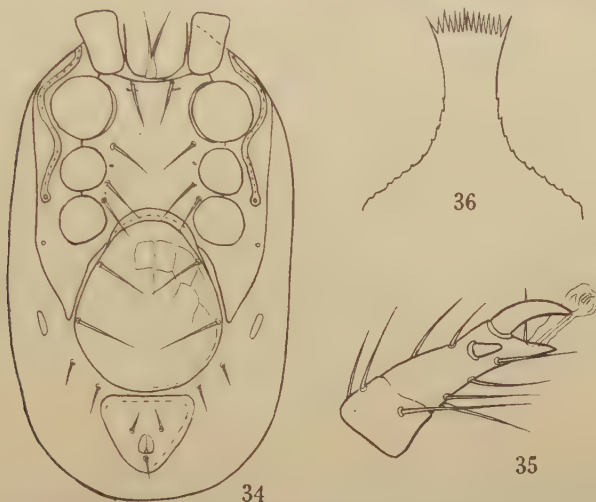
PACHYLAELAPTINI Berlese, A. (1913). *Acarotheca italica*, Firenze, 2.

The pachylaelaptids are readily distinguished from other parasitoids by the sclerotization of the venter. The inter-coxal region in the female is occupied by the fused sternal-endopodal shield which extends posteriorly to the level of coxa IV (fig. 34). A large exopodal-peritrematal shield which may also be fused with the metapodal shields, flanks the geniti-ventral shield (fig. 34). Leg II in the male is heavily armed. Tarsus II in the female may also be provided with stout spurs distally (fig. 35). Two genera have been recorded from Britain, *Pachylaelaps* Berl. and *Sphaerolaelaps* Berl. The former is frequently encountered in humus and soil whilst the latter is myrmecophilous.

* Syn.: *Gamasolaelaptidae* Oudms., 1939 and *Cyrtolaelaptidae* Cooreman, 1943.

Key to genera.

1. Body elongate oval. Tarsus II in both sexes armed with one or more stout spurs distally (fig. 35) *Pachylaelaps* Berlese, 1886.
(Type: *Gamasus pectinifer* G. & R. Canestrini, 1881).
- . Body sub-circular. Tarsus II in both sexes unarmed. *Sphaerolaelaps* Berlese, 1903.
(Type: *Laelaps holothyroides* Leonardi, 1896).



FIGS. 34-36.—*Pachylaelaps* sp. ♀. Fig. 34, venter. Fig. 35, tarsus II. Fig. 36, tectum.

Family PHYTOSEIIDAE Berlese, 1913.

PHYTOSEIINI Berlese, A. (1913). *Acarotheca italica*, Firenze, 11.

The Phytoseiidae comprises a small group of genera characterized by having less than 20 pairs of setae on the dorsal shield in the proto-, deuto-nymphal and adult stages. The majority of the species described have been found with phytophagous mites of the families Tetranychidae ('red-spider mites'), Tenuipalpidae ('false-spider mites') and Eriophyidae ('gall-mites') on a variety of plants. They are chiefly predatory in habit and are considered to be of importance in the control of 'red-spider mites' in orchards, etc. A number of species of *Amblyseius* may also be found in moss and humus.

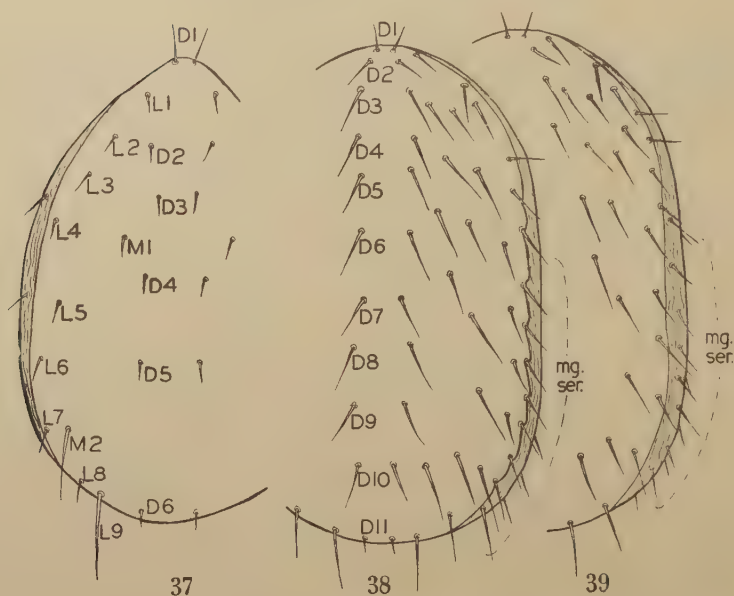
The *Typhlodromus*-group has been revised by Nesbitt (1951) and his work is important since it contains a number of previously unpublished drawings by A. C. Oudemans. Womersley (1954) has recently keyed the known species of the genera *Typhlodromus*, *Phytoseius* and *Amblyseius*. The nomenclature used for the chaetotaxy of the dorsal shield (see fig. 37) is based on Garman (1948).

Key to genera.

Three genera are represented in the British fauna and are separated by the chaetotaxy of the dorsal shield.

1. Dorsal setae in all post-embryonic stages simple or pilose. 2.
- . Dorsal setae, at least a number of the L series, stout and 'thorny'. Only one British species, *Phytoseius macropilis* (Banks), 1906 (= *Seiulus spoofi* Oudms., 1915) *Phytoseius* Ribaga, 1904.
(Type: *Gamasus plumifer* Can. & Fanz., 1876).
2. Setae L 4, M 2 and L 8 whip-like and considerably longer than the other dorsal setae *Amblyseius* Berlese, 1914.
(Type: *Zercon obtusus* C. L. Koch, 1839).
- . Setae L 4, M 2 and L 8 not conspicuously longer than other dorsal setae (fig. 37) *Typhlodromus* Scheuten, 1857*.
(Type: *Typhlodromus pyri* Scheuten, 1857).

* Mr. D. A. Chant, East Malling Research Station, Kent, considers *Kampimodromus* Nesbitt, 1951 to be a synonym of *Typhlodromus*.



FIGS. 37-39.—Examples of the chaetotaxy of the dorsal shield and interseutal membrane in the Phytoseiidae (fig. 37) and Aceosejidae (figs. 38-39). L1-L9 lateral series; D1-D11, dorsal series; mg.ser., marginal series.

Family ACEOSEJIDAE* Baker & Wharton, 1952.

ACEOSEJIDAE Baker, E. W. & Wharton, G. W. (1952). *An Introduction to Acarology*, New York, 58.

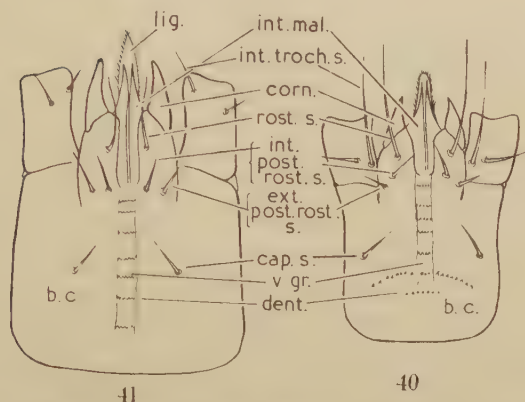
The classification of the Aceosejidae adopted in the present work is based on a revision of the family carried out by the writer and which will be published in detail elsewhere. The major characters used in the following keys are the chaetotaxy of the gnathosoma and the pedipalps, the dorsal shield and interseutal membrane, and the ambulatory appendages. An introduction to the structure of the gnathosoma, dorsal shield and legs has been given above.

The Aceosejidae are commonly encountered in soil and humus; their identification is therefore important to the soil ecologist. The family may be divided into three subfamilies, two of which are represented in the British fauna.

Key to subfamilies.

1. Rostral setae and internal setae on palptrochanter long, whip-like (fig. 40); tarsi II and III, and often IV provided with a pair of long lanceolate setae usually incurved distally (fig. 42); para-anal setae situated in line with the posterior margin of the anus or considerably posterior to the anus; peritrematal shield may extend beyond the posterior margin of coxae IV and the peritreme may be developed posterior to the stigma; median lobe of pulvillus of legs II-IV often lanceolate (fig. 43) PLATYSEIINAE nov.
- , Rostral setae and internal setae on palptrochanter never long and whip-like (fig. 41); tarsi II-IV without specialized setae; peritreme and peritrematal shield normal (fig. 44); para-anal setae normal in position; pulvillus never lanceolate (fig. 43) ACEOSEJINAE nov.

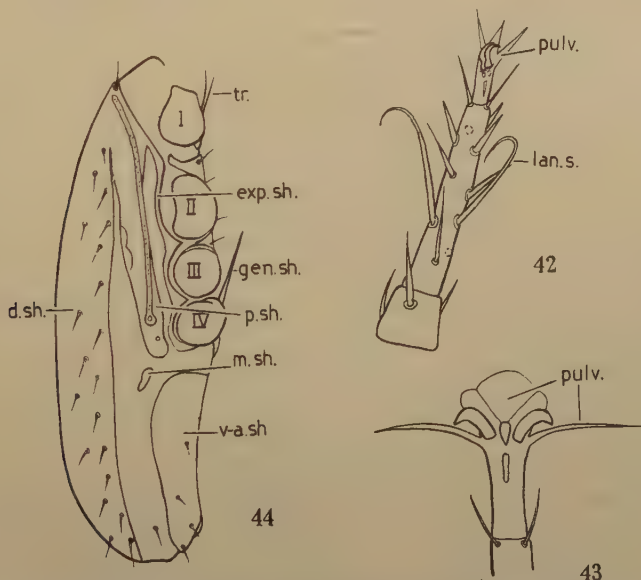
* The concept of this family has been modified to include a number of genera placed by Baker & Wharton in the Phytoseiidae Berl. The Aceosejidae corresponds, in part, with the Seiidae Berl., 1913 nec Berl., 1895.



FIGS. 40-41.—Structure of the venter of the gnathosoma in the Platysejinae (fig. 40) and Aceosejinae (fig. 41).
corn., corniculus; dent., denticles; int.mal., internal malae; int.troch.s., internal trochanter seta; lig., ligula; v.gr., ventral, or capitular groove. Other abbreviations as in figs. 10-11.

Subfamily PLATYSEIINAE NOV.

This subfamily is represented in the British fauna by two genera only, namely, *Platyseius* Berl. (syn.: *Episeius* Hull, 1918) and *Zerconopsis* Hull, 1918. The former usually occurs in damp or wet moss, humus and soil and shows the modification of the pulvillus associated with mites living in wet habitats. The genus *Zerconopsis* is found in humus and rotting wood. The genus *Platyseius* has been keyed by Willmann (1949 a).



FIGS. 42-44.—Fig. 42, tarsus and ambulacral apparatus in *Platyseius* sp. Fig. 43, ambulacral apparatus in *Iphidozercon* sp. Fig. 44, lateral view of an Aceosejid mite. d.sh., dorsal shield; ex.sh., exopodal shield; gen.sh., genital shield; lans.s., lanceolate seta; m.sh., metasternal shield; p.sh., peritrematal shield; pulv., pulvillus; tr., tritosternum; v.-a.sh., ventri-anal shield.

Key to genera.

1. Peritrematal shield strongly developed posterior to coxae IV; peritreme developed posterior to stigma; dorsal shield without 'paddle-like' setae *Platyseius* Berlese, 1916.
(syn.: *Episeius* Hull, 1918).
(Type: *Lasioseius* (*Platyseius*) *capillatus* Berl., 1916).
- . Peritrematal shield not extending posterior to coxae IV; peritreme normal; dorsal shield with three pairs of 'paddle-like' setae (fig. 27 i)..... *Zerconopsis* Hull, 1918.
(Type: *Gamasus remiger* Kramer, 1876).

Subfamily ACEOSEJINAE nov.

This subfamily contains the bulk of the British *Aceosejidae*. Some species of the genera *Lasioseius* Berl., *Jordensia* Oudms. (syn.: *Chamolaelaps* Hull in Turk & S. Turk, 1951), *Garmania* Nesbitt and *Blattisocius* Keegan have been keyed and figured by Nesbitt (1951). The genera included in the following key will be dealt with in detail in the work referred to above.

Key to genera.

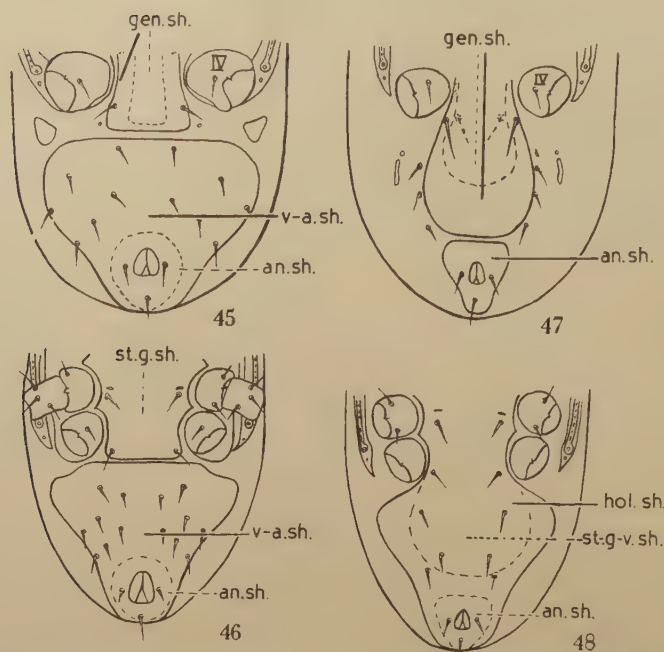
1. Genital shield narrow, without genital setae, the latter being situated lateral to the shield on the interscutal membrane (fig. 45) 2.
- . Genital shield normal with a pair of genital setae (fig. 45) .. 3.
2. Dorsal shield incompletely covering the dorsum of the mite and with lateral incisions. In moss, humus, etc. *Arctoseius** Sig Thor, 1930.
(syn.: *Tristomus* Hughes, 1948).
(Type: *Arctoseius laterincisus* Sig Thor, 1930).
- . Dorsal shield completely covering dorsum of the mite and without lateral incisions *Iphidozercon* Berlese, s. lat.
(a) Dorsum strongly arched along the mid-dorsal line.. *Iphidozercon* Berl., 1903.
(b) Dorsal shield not arched in the mid-dorsal line..... *Arctoseiopsis* Evans, 1954.
(Type: *Seiulus minutus* Halbert, 1915).
3. Dorsal shield incised laterally; with ventri-anal shield.. 4.
- . Dorsal shield without trace of lateral incisions; with anal or ventri-anal shield 5.
4. Dorsal shield with deep lateral incisions; dorsal series comprising ten pairs of setae; lateral interscutal membrane with five setae; sternal shield with the normal three pairs of setae. Intertidal, associated with *Balanus*. *Arctoseiodes* Willmann, 1949.
(Type: *Arctoseius* (*Arctoseiodes*) *ibericus* Willm., 1949).
- . Dorsal shield with weak lateral incisions; dorsal series comprising eleven pairs of setae; lateral interscutal membrane with ten or eleven setae; sternal shield with two pairs of setae (h l on small shield or on membrane). On the seashore or in humus..... *Leioseius* Berlese, 1916.
(Type: *Ameroseius minusculus* Berl., 1905).
5. Marginal setae situated on the dorsal shield (fig. 38)..... 6.
- . Five to eight marginal setae situated on the lateral interscutal membrane (fig. 39) 9.
6. Dorsal setae plumose, clavate or serrulate 7.
- . Dorsal setae simple or pilose 8.
7. Dorsal shield with twenty-nine pairs of setae, dorsal series comprising eight pairs; corniculi forked distally. In vegetable debris often associated with acarid mites. Predatory or mycetophilous..... *Kleemannia* Oudemans, 1930.
(Type: *Zercon parvidus* C. L. Koch, 1839).
- . Dorsal shield with thirty-four pairs of setae, dorsal series comprising ten pairs; corniculi normal. In humus, etc. Monotypical..... *Zercoseius* Berlese, 1916.
(Type: *Seius spathuliger* Leonardi, 1899).

* Keyed by Willmann (1949).

8. With a large ventri-anal shield occupying almost all the region posterior to coxae IV, its anterior margin concave; exopodal shields entire or fragmented. In humus or moss (Type: *Seiulus levis* Oudemans & Voigts, in Voigts & Oudemans 1904). *Neojordensia* nov.
- With anal shield remote from genital shield; corniculi sometimes sinuous (e.g. *Jordensia hypudaei* (Oudms.) 1902). Predatory (?) on acarids, etc. In stored food products and in nests of birds and small mammals *Jordensia* Oudemans, 1937.
(Type: *Gamasus cossi* Dugès, 1834).
9. With anal shield remote from genital shield; sclerotization weak. Associated with acarids in food products and in dwelling houses. Monotypical *Garmania* Nesbitt, 1951.
(Type: *Typhlodromus domesticus* Oudms., 1929).
- With well-developed ventri-anal shield 10.
10. Fixed digit of the chelicerae reduced; peritreme not extending beyond the anterior margin of coxae II. Associated with insects in cultures, etc. *Blattisocius* Keegan, 1944.
(Type: *Blattisocius tridons* Keegan, 1944 = *Typhlodromus tineivorus* Oudms., 1929 = *Lasioseius dentriticus* Berl., 1918).
- Both digits of the chelicerae normal; peritreme extending beyond the anterior margin of coxae I 11.
11. With jugularia; lateral interscutal membrane with eight or more setae; posterior dorsal setae long and spinose. On large fungi *Aceosejus* Sellnick, 1941.
(Type: *Sejus muricatus* C. L. Koch, 1839, nec. *Seius muricatus* Berl., 1887).
- Without jugularia; lateral interscutal membrane with six or more lateral setae; dorsal setae simple, pilose or serrulate. In humus, moss, on bark of trees, predatory (?) on other mites in stored foodstuffs etc. *Lasioseius* Berlese, s. lat.
(a) Fixed digit of the chelicera in both sexes multi-dentate (with a row of closely-set teeth); body usually well-sclerotized *Lasioseius* Berlese, 1916, s. str.
(syn.: *Borinquolaclaps*, Fox 1946).
(Type: *Seius muricatus* Berl, 1887 nec C. L. Koch, 1839 = *Typhlodromus berlesei* Oudms., 1938 syn.: *Lasioseius aba* Baker & Wharton, 1952).
- (b) Fixed digit of the chelicera in both sexes at the most with two or three well-separated teeth; body weakly sclerotised *Paragarmania* Nesbitt, 1951.
(Type: *Typhlodromus mali* Oudemans, 1929).

Males.

1. Dorsal shield with lateral incisions 2.
- Dorsal shield without trace of lateral incisions 4.
2. With small shields between sterniti-genital and ventri-anal shields 3.
- Without shields between geniti-ventral and sterniti-genital anal shields *Arctoseius* Sig Thor, 1930.
3. Lateral incisions strong; dorsal series with ten pairs of setae *Arctoseiodes* Willmann, 1949.
- Lateral incisions weak; dorsal series with eleven pairs of setae *Leioseius* Berlese, 1916.
4. Marginal setae on the dorsal shield *Jordensia* Oudemans, 1937.
- Five to eight marginal setae on interscutal membrane 5.
5. Dorsal setae clavate, plumose or serrulate 6.
- Dorsal setae simple, spinose or pilose 7.
6. Corniculi forked distally; dorsal series with only eight pairs of setae *Kleemannia* Oudemans, 1930.
- Corniculi normal; dorsal series with ten pairs of setae .. *Zercoeseius* Berlese, 1916.
- Ventri-anal shield with a cone-shaped, strongly sclerotized protuberance near the anterior border *Aceosejus* Sellnick, 1941.
- Ventri-anal shield without conical protuberance 8.
8. Dorsal shield completely covering dorsum of mite; small species, about 250-300 μ in length *Iphidozercon* Berlese, 1903
- Dorsal shield not completely covering dorsum of mite; larger species, about 400-600 μ in length *Lasioseius* Berlese, 1916.



FIGS. 45-48.—Diagrammatic representations of the types of genital, ventral and anal shields encountered in some of the Aceosejidae, Eviphididae and Laelaptidae. Fig. 45, Aceosejidae, females. Fig. 46, Aceosejidae and Eviphididae males. Fig. 47, Laelaptidae, females. Fig. 48, Laelaptidae, males.
an.sh., anal shield; hol.sh., holoventral shield; st.g.sh., sterniti-genital shield; st.g.-v.sh., sterniti-geniti-ventral shield.

Family DIGAMASELLIDAE nov.

ALLOLAELAPTIDAE* Oudemans, A. C. (1939). *Zool. Anz.* 126, 23 (in part).

ASCAIDAE† Oudemans, Baker, E. W. & Wharton, G. W. (1952). *An Introduction to Acarology*, New York, 63.

The mites included in this family are closely related to the Aceosejidae but are distinguished from them by the presence of two dorsal shields of approximately equal size in the adult and nymphal stages and the armature of leg II in the male. The Digamasellidae is represented by two genera in the British fauna; all the species are less than 400 μ in length and occur in soil, humus, etc. The genus *Digamasellus* has been revised by Leitner (1949).

Key to genera.

1. Posterior dorsal shield in both sexes with a pair of conspicuous setae-bearing 'horns' postero-laterally..... *Asca* v. Heyden, 1876.
(Type: *Acarus aphidioides* Linn., 1758).
- , Posterior dorsal shield in both sexes without setae-bearing 'horns' postero-laterally..... *Digamasellus* Berlese, 1905.
(Syn.: *Dendrolaelaps* Halbert, 1923).
(Type: *Gamasellus* (*Digamasellus*) *perpusillus* Berl., 1905).

* According to Article IV of the International Rules of Zoological Nomenclature (1926) this family name is invalid.

† The subfamily Ascainae Voigts & Oudms., 1905 was proposed, without definition, for *Asca* (v. Heyden) Voigts & Oudms., 1905 nec *Asca* v. Heyden 1826. The three species listed under *Asca* v. Heyden by Voigts *et al.* are not congeneric with each other nor is any one of them congeneric with the genotype of *Asca* v. Heyden, 1826.

Family EVIPHIDIDAE Berlese, 1913.

EVIPHIDINI Berlese, A. (1913). *Acarotheca italica*, Firenze, 2.

The species included in this family may be distinguished in the male by the presence of a sterniti-genital shield separate from an anal shield. The females show a superficial resemblance to the *Aceosijidae* (see p. 216). Four genera are represented in the British fauna.

Key to subfamilies.

1. Dorsal shield poorly sclerotized in the female but well-sclerotized in the male and nymphae; sternal shield not sclerotized in the female; palpgenu with only five setae in both sexes *Thinoseiinae* Evans.
- Dorsal shield well-sclerotized in both sexes; sternal shield sclerotized in the female; both sexes with six setae on the palpgenu *Eviphidinae* Berlese.

Subfamily THINOSEIINAE Evans, 1954.

This subfamily contains only one genus, *Thinoseius* Halbert, 1920 (type: *Thinoseius berleseii* Halbt., 1920 = *Lasioseius fucicola* Halbt., 1920) which is intertidal in distribution. The genus has been revised by Evans (1954).

Subfamily EVIPHIDINAE Berlese, 1913.

This subfamily is represented by the following three genera :

Key to genera.

1. Peritrematal shield strongly developed posterior to coxae IV in both sexes and may be fused with metapodal shields; dorsal shield strongly sclerotized and usually arched; * tectum elongate, denticulate (fig. 17). In humus, decaying wood, etc. *Eviphis* Berlese, 1903.
(syn.: *Copriphis* Berl., 1910).
(Type: *Eumaeus pyrobolus* C. L. Koch, 1839).
- Peritrematal shield not developed posterior to coxae IV; dorsal shield not arched 2.
2. Tectum produced into an elongate process; interscutal membrane posterior to coxae IV with a few simple setae. In compost heaps, etc., immature stages often transported by insects *Alliphis* Halbert, 1923.
(Type: *Gamasus halleri* G. & R. Canestrini, 1881).
- Tectum not produced into an elongate process; anal shield considerably longer than wide; interscutal membrane posterior to coxae IV with numerous short, stout, spine-like setae. In bee-hives *Melittiphis* Berlese, 1918.
(Type: *Laelaps (Iphis) alvearius* Berl., 1895).

Family LAELAPTIDAE Berlese, 1892.

LAELAPTIDAE Berlese, A. (1892). *Acari Myriopoda et Scorpiones* (Ordo Mesostigmata), 30.

The classification of the Laelaptidae is extremely complex in view of the wide variety of structures exhibited by the forms included therein: especially by those which have adopted a parasitic mode of life. Parasitic forms may show a decrease in the sclerotization of the dorsal and ventral shields, a modification of the chelicerae for piercing the skin of the host and a reduction in the form of the tritosternum. Within recent years there has been increasing interest in the systematics of the parasitic groups which may prove to be vectors of disease to man. This has resulted in the classification of the Laelaptidae being based on the specialized parasitic forms

* The specimen should be orientated in a fluid medium, e.g. lactic acid, to observe this character.

without any attempt to relate them to the more numerous free-living species. The classification adopted in the present work follows, in the main, that proposed by Evans (1955 b). In the present state of our knowledge of the Laelaptidae a practical classification of this nature appears to be the most satisfactory.

A key to the subfamilies of the Laelaptidae.

- | | | |
|---|----|---------------------------|
| 1. Tritosternum normal with well-developed lacinae; stigmata ventro-lateral. Free-living, commensals or ectoparasites | 2. | |
| - Tritosternum rudimentary (never bipartite) or absent; stigmata often dorsal or dorso-lateral. Endoparasites of reptiles, birds and mammals or ectoparasites of bats (<i>Chiroptera</i>) | 5. | |
| 2. Chelicerae in the females chelate-dentate (except in some species of <i>Haemogamasus</i> , <i>Laelaspis</i> * and <i>Holostaspis</i>); body well-sclerotized | 3. | |
| - Chelicerae in the females shear-like (without teeth) or stylet-like (fig. 9); dorsal and ventral shields weakly sclerotized; dorsal shield may be divided. Ecto-parasites of reptiles, birds and mammals | 4. | |
| 3. Dorsal and ventral shields with a moderate covering of setae; proto- and deuto-nymphal stages with divided dorsal shield. Free-living or ecto-parasitic | | LAELAPTINAE Berlese. |
| - Dorsal and ventral shields and interscutal membranes densely clothed with setae. Dorsal shield in the proto- and deuto-nymphal stages with an undivided dorsal shield. Inhabitants of the nests of birds and mammals. | | HAEMOGAMASINAE Oudemans. |
| 4. Chelicerae shear-like in females | | LIPONYSSINAE Ewing. |
| - Chelicerae stylet-like in females | | DERMANYSSINAE Kolenati. |
| 5. Ecto-parasites of bats (<i>Chiroptera</i>) | | SPINTURNICINAE Oudemans. |
| - Parasites of the respiratory tract of mammals | | HALARACHNINAE Oudemans. |
| - Parasites of the respiratory tract of reptiles | | ENTONYSSINAE Ewing. |
| - Parasites of the nasopharynx of birds | | RHINONYSSINAE Trouessart. |

Subfamily LAELAPTINAE Berlese, 1892.

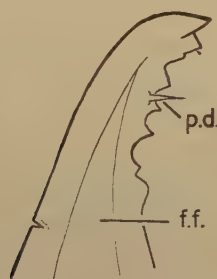
The LAELAPTINAE (syn.: HYPOASPIDINAE Vitzthum) are found in a variety of habitats e.g. in moss, humus, in debris of nests and on small mammals. Those species parasitizing small mammals or associated with ants show a modification of the chelicerae. In the former both digits of the chelicerae of the male are of the form shown in fig. 8, whereas in the latter the dentition of the chelate chelicerae in both sexes is rudimentary or absent. The generic concept within the subfamily requires radical revision. Seven genera are represented in the British fauna.

Key to genera.

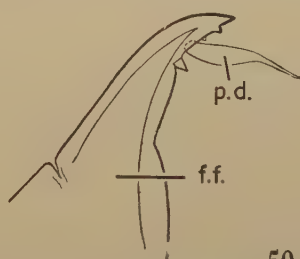
- | | | |
|--|----|--|
| 1. Femur and genu II in both sexes with distinct thumb-like or conical spurs (cf. fig. 27 h). Parasites of small mammals | | <i>Androlaelaps</i> Berlese, 1903.
(syn.: <i>Turkiella</i> Zumpt & Till, 1954).
(Type: <i>Laelaps hermaphrodita</i> Berl., 1903). |
| - Leg II in the female without spurs, at the most with strong spines | 2. | |
| 2. Geniti-ventral shield with more than ten pairs of setae; metapodal shields large, triangular. Predatory, in nests of small mammals, etc. | | <i>Eulaelaps</i> Berlese, 1903.
(syn.: <i>Hemilaelaps</i> Hull, 1918).
(Type: <i>Laelaps stabularis</i> C. L. Koch, 1839 — <i>Laelaps pachypus</i> Hermann, 1804). |
| - Genital or geniti-ventral shield with less than six pairs of setae | 3. | |

* These genera may be separated from the Liponyssinae and Dermanyssinae by the presence of strongly sclerotized dorsal and ventral shields.

3. Chelicerae in both sexes chelate but teeth rudimentary or absent*. Myrmecophilous 4.
- . Chelicerae at least in the female chelate-dentate 5.
4. Tectum produced in a long acute process; corniculi weak; dorsal setae of moderate length *Holostaspis* Kolenati, 1858.
(Type: *Holostaspis isotricha* Kol., 1858).
- . Anterior margin of tectum rounded; corniculi well-sclerotized; dorsal setae long *Laelaspis* Berlese, 1903.
(Type: *Iphis astronomicus* Berl., 1889).
5. Both sexes with two very long spine-like setae dorsally on femur I; female with geniti-ventral shield; chelicerae chelate-dentate in the females but modified, as in *Haemolaelaps*, in the male. Parasitic on small mammals *Laelaps* C. L. Koch, 1839.
(Type: *Acarus muris* Ljungh, 1799 = *L. agilis* Koch, 1839).
- . Both sexes without long spine-like setae on femur I 6.
6. Podal-peritrematal shield strongly developed posterior to coxa IV; geniti-ventral shield large and about as broad as long; tectum strongly sclerotized, trispinate. The species included in this genus bear a superficial resemblance to *Eulaelaps*. In soil, humus, etc. *Pseudolaelaps* Berlese, 1916.
(syn.: *Hoplolaelaps* Berl., 1910 nec Berl., 1903).
(Type: *Laelaps* (*Hoplolaelaps*) *doderói* Berl., 1910).
- . Podal-peritrematal shield not strongly developed posterior to coxa IV; females with a genital shield or rarely a geniti-ventral shield considerably longer than broad.... 7.
7. *Pilus dentilis* normal, piliform, in both sexes (fig. 49); chelicerae of the male chelate-dentate and with a strong spermatophoral process *Hypoaspis* G. Canestrini, s. lat.
(a) Dorsal setae simple or pilose b.
-. Dorsal setae spatulate or clavate *Cosmolaelaps* Berlese, 1903.
(Type: *Laelaps claviger* Berl., 1883).
- b. Lateral and ventral interscutal membranes richly provided with setae; sternal setae long. On *Bombus* spp. *Pneumolaelaps* Berlese, 1920.
(Type: *Iphis bombicolens* G. Can., 1885).
- . Lateral and interscutal membranes with moderate covering of setae. Predatory on other arthropods in moss, humus, soil or nest debris *Hypoaspis* G. Can., 1885, s. str.
(Type: *Hypoaspis krameri* G. & R. Can., 1881).
- . *Pilus dentilis* strongly developed in the female, inflated (fig. 50); chelicerae greatly modified in the male (fig. 8) *Haemolaelaps* Berlese, 1910.
(Type: *Laelaps* (*Haemolaelaps*) *marsupialis* Berl., 1910).



49



50

FIGS. 49-50.—Structure of the *pilus dentilis* in *Hypoaspis* sp. ♀ (fig. 49) and *Haemolaelaps* sp. ♀ (fig. 50).
f.f., fixed finger; p.d., *pilus dentilis*.

Subfamily HAEMOGAMASINAE Oudemans, 1926.

The species included in this subfamily may be readily recognized by the dense setation of the dorsal and ventral shields, and the interscutal membrane. They are essentially inhabitants of the nests of birds and small mammals where they may occur in enormous numbers. The Haemogamasinae has recently been revised by

* See footnote on p. 230.

Keegan (1951). Only one genus, *Haemogamasus*, which may be divided into the following two subgenera, is represented in the British fauna :

1. Sternal shield in the female with accessory setae, i.e. more than the usual three pairs *Haemogamasus* Berlese, 1889, *s.str.*
(Type : *Haemogamasus hirsutus* Berl., 1889).
- , Sternal shield in the female with the normal three pairs of setae only *Eruhaemogamasus* Ewing, 1933.
(Type : *Eruhaemogamasus onychomydis* Ewing, 1933 = *Dermanyssus ambulans* Thorell, 1872).

Subfamily LIPONYSSINAE Ewing, 1923.

This subfamily includes the majority of laelaptids which are ectoparasitic on reptiles, birds and mammals. They all show a modification of the chelicerae in both sexes and, with the exception of *Myonyssus*, a reduction in the sclerotization of the body. Most of the forms have probably arisen from species now included in the Laelaptinae but there is such strong convergence in the family as a whole that the true relationship between the free-living and parasitic species is extremely difficult to elucidate. There has been a tendency to subdivide the Liponyssinae into a large number of genera on the basis of minor details of morphology as, for example, Fonseca (1948) has done. Future investigations will probably result in the synonymising of a large number of these genera.

Eight genera are represented in the British fauna—*Lepronyssus* Kol., 1858 is considered a synonym of *Ichoronyssus* Kol. and *Bdellonyssus* Fonseca, 1948 and *Fonseconyssus* Radford, 1950, synonyms of *Ornithonyssus* Sambon. *Ornithonyssus bacoti* (Hirst) 1913, the tropical rat mite, and *Ornithonyssus sylvarum* (Can. & Fanz.) 1877, the European fowl mite are both reported to bite humans.

Key to genera.

1. Dorsal shield in the female divided 2.
- , Dorsal shield in the female undivided 3.
2. Posterior dorsal shield minute (fig. 26) ; sternal shield in the female with only two pairs of setae ; male with a separate anal shield. Ecto-parasites of reptiles in vivaria. *Ophionyssus* Mégnin, 1884.
(syn. : *Serpenticola* Ewing, 1923).
(Type : *Dermanyssus natricis* Gervais, 1844).
- , Posterior dorsal shield well-developed ; sternal shield in the female with three pairs of setae ; male with separate ventri-anal shield. On birds and mammals *Steatonyssus* Kolenati, 1858.
(Type : *Acarus musculi* Schrank, 1803).
3. Female with a geniti-ventral shield bearing more than three pairs of setae 4.
- , Female with genital shield with one pair of setae 5.
4. Strongly sclerotized species with the dorsal shield completely covering the dorsum of the mite ; anal shield large, broad, often with accessory setae ; male with holovenital shield *Myonyssus* Tiraboschi, 1904.
(syn. : *Tetragonyssus* Ewing, 1923).
(Type : *Myonyssus decumani* Tiraboschi, 1904).
- , Dorsal shield not completely covering the dorsum of the mite ; anal shield pear-shaped ; sternal shield with large circular ornamented areas between h1 & h2 *Hirstesia* Fonseca, 1948.
(Type : *Liponyssus sternalis* Hirst, 1921).
5. Both sexes with a dorsal spine on coxae II only 6.
- , Both sexes also with posteriorly directed spines on coxae II, III and sometimes IV *Hirstionyssus* Fonseca, 1948.
(Type : *Dermanyssus arcuatus* C. L. Koch, 1839).
6. Genital shield more or less parallel-sided ; segments of legs elongate *Macronyssus* Kolenati, 1858.
(Type : *Caris longimana* Kol., 1856).
- , Genital shield gradually tapering posteriorly 7.
7. Legs stout ; male with a separate ventri-anal shield *Ichoronyssus* Kolenati, 1858.
(Type : *Dermanyssus scutatus* Kol., 1856).
- , Legs elongate, normal ; male with holovenital shield. *Ornithonyssus* Sambon, 1928.
(Type : *Leiognathus sylvarum* Can. & Fanz., 1887).

Subfamily DERMANYSSINAE Kolenati, 1859.

These are laelaptid mites with the chelicerae stylet-like (modified for piercing the skin of the host). The body in both sexes is weakly sclerotized. There is only one British genus, namely *Dermanyssus* Dugès, 1834 (Type: *Acarus gallinae* Degeer, 1778). The common species of this genus in Britain is *D. gallinae*, commonly known as the 'red mite of poultry'. It also occurs on a number of species of wild birds and has been reported biting humans.

Subfamily SPINTURNICINAE Oudemans, 1901.

In Britain, species of this subfamily have been recorded from bats only. The dorsal and ventral shields are markedly reduced and the stigmata are located dorsally. The position of the stigmata (and part of the peritreme) on the dorsal surface is probably the result of the enlargement of the coxae and the dorso-ventral compression of the body. The legs and the ambulacral apparatus are strongly formed. Two genera are recorded from Britain. The British species of the Spinturnicinae have been keyed by Turk (1946).

Key to genera.

1. With a single dorsal shield; body tapering posteriorly, not extending beyond legs IV *Spinturnix* v. Heyden, 1826.
(syn.: *Pteroptus* Dufour, 1832 and *Diplostaspis* Kol., 1857).
Type: *Spinturnix myoti* Kol., 1856).
- . With two dorsal shields; body lobate posteriorly and extending beyond legs IV *Periglischrus* Kolenati, 1857.
(Type: *Periglischrus caligus* Kol., 1857).

Subfamily HALARACHNINAE Oudemans, 1906.

The mites included in this subfamily are parasites (endoparasites) of the respiratory tract of the *Pinnipedia* and some other mammals. As endoparasites they display marked modifications in the structure of the chelicerae, the degree of sclerotization of the body and the form of the stigmata and peritremes. The chelicerae have the movable digit more strongly developed than the fixed digit. The dorsal and ventral plates are also strongly reduced. There is a marked reduction in the chaetotaxy of the pedipalps and the palptibia and palptarsus are fused into a tibio-tarsus. The stigmata are situated laterally but the peritreme is minute. The tristosternum is absent.

Two genera have been recorded from Britain. The genus *Halarachne* Allman, 1847 (syn.: *Rhinixodes* Nehring, 1884 and *Rhinacarus* Nehring, 1884) is represented by the type species, *Halarachne halichoeri* All. and has been recorded from *Halichoerus grypus* (Fabr.), the grey seal. The other genus, *Pneumonyssus* Banks, 1901 (syn.: *Pneumotuber* Landois & Hoepke, 1914) represented by the type species, *Pneumonyssus simicola* Banks, 1901 has been recorded from the lungs of a Rhesus monkey in the Zoological Society's Gardens, London.

The Halarachninae has been revised by Newell (1947).

Subfamily ENTONYSSINAE Ewing, 1923.

Mites of this subfamily are parasites in the lungs of snakes. The body is more heavily sclerotized than in the Halarachninae, but the chelicerae are very specialized. They have been recorded from African and American snakes in vivaria. Turk (1947) has reviewed the generic concept in this subfamily.

Subfamily RHINONYSSINAE Trouessart, 1895.

The Rhinonyssinae are found in the nasopharynx of birds and distributed all over the world. The body is weakly sclerotized with the reduced dorsal shield showing

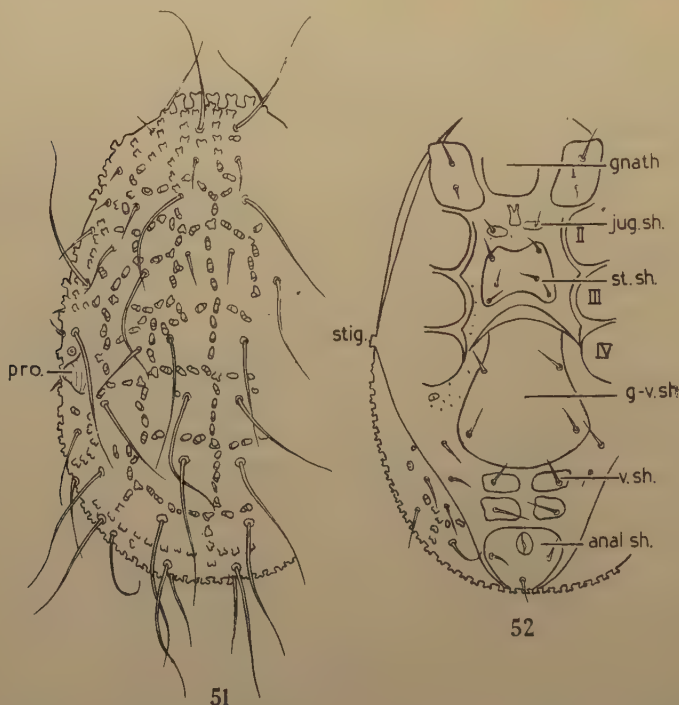
various degrees of fragmentation. The tritosternum is absent and the stigmata are situated laterally or dorsally and may or may not be provided with short peritremes. All legs are well-developed and usually terminate in strongly formed claws.

Four genera are recorded from Britain. Two of these are new records, namely, *Sternostoma* Berl. & Trouessart (syn. *Sternostomum* Trouessart, 1895 nec *Sternostomum* Turk, 1951) represented by *Sternostoma tracheacolum* Lawrence, 1948 from the tracheae of canaries, and *Rhinoecius* Cooreman, 1948, represented by the genotype, from the Long-eared Owl.

This subfamily has been revised recently by Castro (1948) and Strandtmann (1948).

Key to genera.

1. Stigmata situated dorsally (or laterally) and without peritremes 2.
- . Stigmata situated dorsally and provided with peritremes. 3.
2. With distinct posterior dorsal shield; sternal shield present; claws on tarsus I rudimentary or absent *Sternostoma* Berlese & Trouessart, 1889.
(Type: *Sternostoma cryptorhynchum* Berl. & Trouess., 1889).
- . Without well-developed posterior dorsal shield; sternal shield lacking; claws on tarsus I well-developed *Rhinonyssus* Trouessart, 1894.
Type: *Rhinonyssus conviventris* Trouess., 1894).
3. Both digits of the chelicera minute but equally well-developed *Ptilonyssus* Berlese & Trouessart, 1894.
(Type: *Ptilonyssus echinatus* Berlese & Trouessart, 1889).
- . Chelicera without fixed digit *Rhinoecius* Cooreman, 1946.
(Type: *Rhinoecius oli* Cooreman, 1946).



FIGS. 51-52.—Structure of the dorsum (fig. 51) and venter (fig. 52) of *Epicrius canestriini* Haller, ♀.
gnath., gnathosoma; g-v.sh., genito-ventral shield; jug.sh., jugular shields; pro., protuberance; stig., stigma; v.sh., ventral shield.

MESOSTIGMATA-EPICRIOIDEA

The epicrioids are distinguished from the parasitoids by the location of the genital orifice and the structure of the chelicerae in the male. The females are basically very similar in both groups but, in the species recorded from Britain, may be distinguished by the characteristic form of the shield or shields covering the dorsum. Two families are represented in the British fauna. The classification adopted in this work follows that proposed by Evans (1955).

Key to families.

1. Dorsal shield, entire in both sexes, with a polygonal network of bi- or tri-furcate tubercles and a dorso-lateral protuberance (fig. 51); dorsal setae simple, pilose or strongly barbed (fig. 53); both sexes with jugularia, sternal shield in the female showing various degrees of fragmentation; female with large geniti-ventral shield; peritreme strongly reduced and enclosed with the stigma in the lateral extension of the dorsal shield; leg I without ambulacral apparatus but with conspicuous clubbed setae (fig. 56); palptarsal seta three-pronged. EPICRIIDAE Berlese.
- Dorsal shield in both sexes divided into two shields of approximately equal size, lateral margins of the shields serrated (fig. 60); dorsal setae simple, pilose or serrated; sternal shield in the female undivided, in the male often with jugularia; female with truncated genital shield; both sexes with reduced peritreme and well-developed peritrematal shield; leg I with ambulacral apparatus but without clubbed setae; palptarsal seta with two prongs; coxa II with an anteriorly directed spur. ZERCONIDAE Berlese.

Family EPICRIIDAE Berlese, 1885.

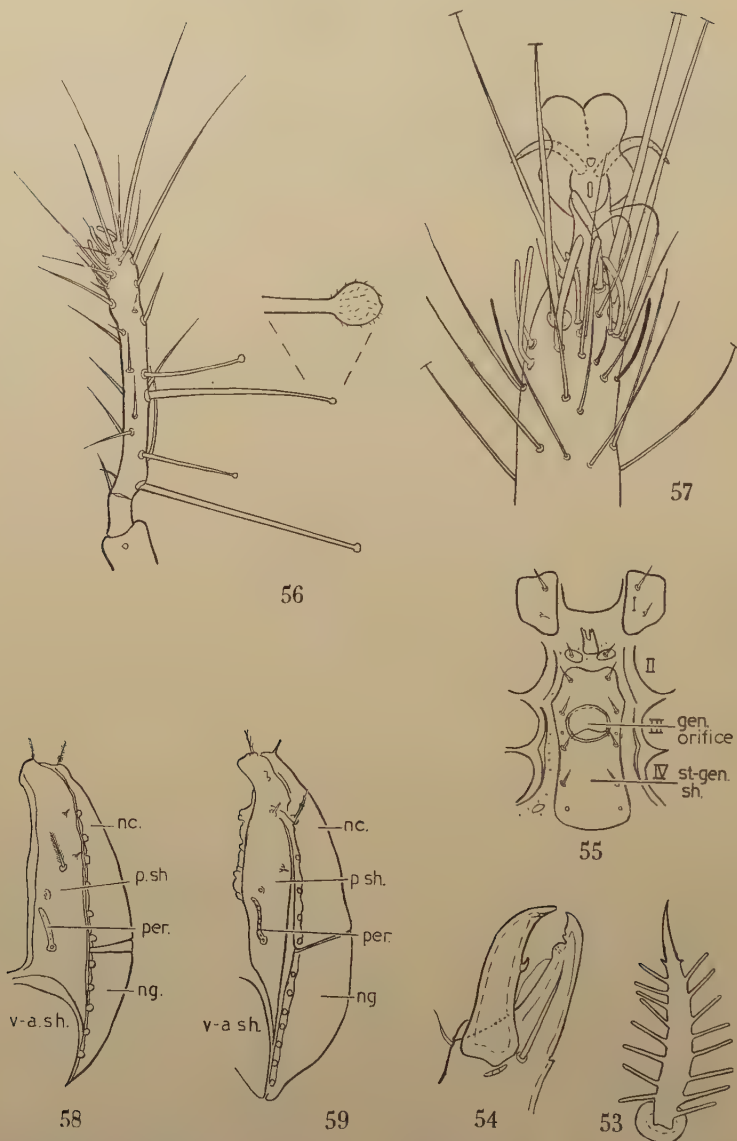
EPICRIIDAE Berlese, A. (1885). *Bull. Soc. ent. Ital.*, 17, 129.

The mites of this family are readily distinguished from all other mesostigmatids by the ornamentation of the dorsal shield in both sexes. The small tubercles from a geometric pattern completely covering the dorsal shield (fig. 51). The function of the dorsal protuberances is not known. The dorsal setae may be long and pilose or short and strongly barbed (figs. 51 & 53). The chelicerae are fundamentally the same in both sexes; the chelicerae in the male being without a spermatophoral process (fig. 54). The gnathosomal setae are arranged as in the Parasitoidea. The genital orifice in the male is situated between coxae III and closed by two shields, the anterior of which bears a pair of simple setae (fig. 55).

Only two genera are at present recognized in this family and both are represented in Britain. These genera have been revised recently by Evans (1955 a).

Key to genera.

1. Majority of the dorsal setae more than 100 μ in length, simple or pilose; dorso-lateral protuberance large, conspicuous; tarsus I with three or more clubbed setae. In moss, humus and decaying bark of trees *Epicrius* G. Canestrini & Fanzago, 1877.
(syn.: *Eugamasus* Absolon, 1899, *Diepicrius* Berl., 1916 and *Epicriella* Willmann, 1953).
(Type: *Epicrius geometricus* G. Canestrini & Fanzago, 1877=*Gamasus mollis* Kramer, 1876).
- Dorsal setae less than 70 μ in length, stout and barbed (fig. 53); tubercles more numerous; dorso-lateral protuberance weak; tarsus I with less than three clubbed setae. In humus *Berlesiana* Turk, 1943.
(Type: *Epicrius cirratus* Berl., 1916).



FIGS. 53-59.—Fig. 53, dorsal seta of *Berlesiana denticulata* Evans. Fig. 54, chelicera of *Epicrius mollis* (Kramer). Fig. 55, sterniti-genital region in the male of *Epicrius canestrinii* Haller. Fig. 56, chaetotaxy of tarsus I of *E. mollis*, ♀. Fig. 57, distal half of tarsus I of *Zercon triangularis* Koch, ♀. Fig. 58, lateral view of *Parazercon radiatus* (Berlese). Fig. 59, lateral view of *Prozercon trågårdhi* (Halbert).
 gen. orifice, genital orifice; nc., notocephale; ng., notogaster; p. peritreme; p.sh., peritrematal shield; st-gen.sh., sterniti-genital shield.

Family ZERCONIDAE Berlese, 1892.

ZERCONIDAE Berlese, A. (1892). *Acari Myriopoda et Scorpiones* (Ordo Mesostigmata), 74.

The Zerconidae may be distinguished from the Epicriidae by the divided dorsal shield in both sexes and the truncated genital shield in the female. The Zerconids are broadly triangular in shape with the lateral margins serrated (fig. 60). Other characters of importance have been mentioned in the above key to families.

Sellnick (1944) in his revision of the genus *Zercon* C. L. Koch has used the chaetotaxy and arrangement of pores on the posterior dorsal shield (or notogaster) for separating the species. The nomenclature used by Sellnick is given in fig. 60.

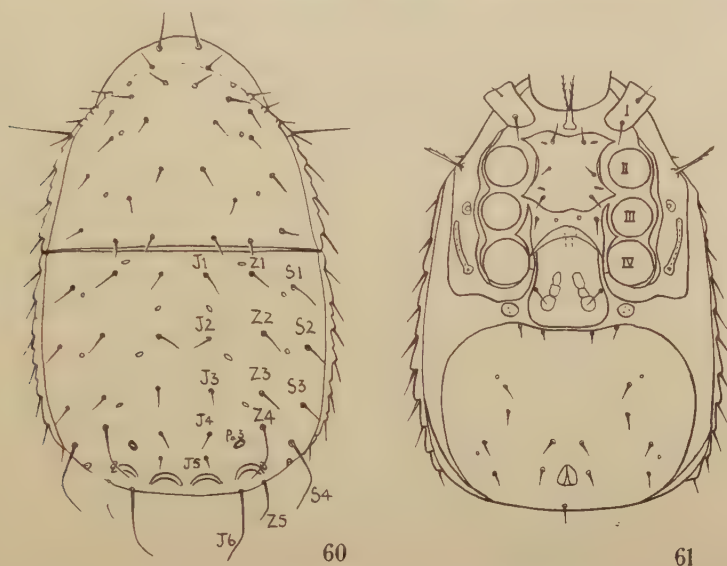


FIG. 60-61.—Dorsum (Fig. 60) and venter (Fig. 61) of *Zercon blesti* Evans. J 1-J 6, dorsal setae; Z 1-Z 5, median setae; S 1-S 4, lateral setae; Po. 3, pore 3.

Three genera* are encountered in the British fauna and may be separated as follows:

Key to genera.

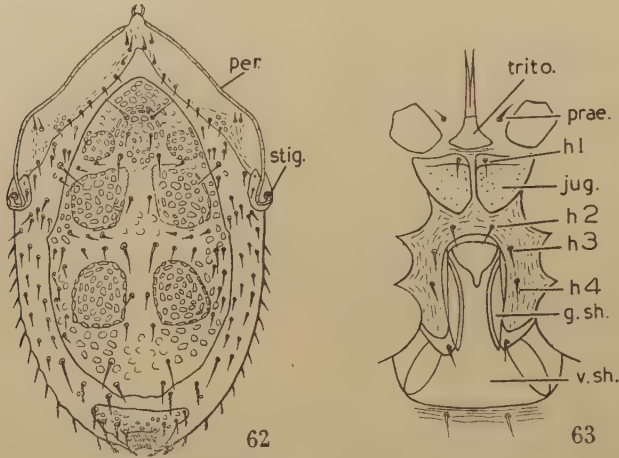
1. Anterior dorsal shield in both sexes sloping gradually towards its anterior margin; peritrematal shield not extending a great distance posterior to coxa IV and not flanking the ventri-anal shield; peritrematal shield with a single seta (fig. 61). Common in moss, humus, etc. *Zercon* C. L. Koch, 1841.
(syn.: *Triangulazercon* Jacot, 1938).
(Type: *Zercon dimidiatus* Koch, 1841 = *Zercon triangularis* Koch, 1836).
2. Anterior dorsal shield in both sexes sloping abruptly before the vertical setae (figs. 58 & 59); peritrematal shield extending posterior to coxa IV and flanking part of the ventri-anal shield; peritrematal shield with more than one seta. 2.
2. Peritrematal shield with one large and two small setae (fig. 58); marginal setae filamentous; posterior dorsal depressions indistinct or absent. Similar in habitat but not as common as *Zercon* *Parazercon* Trägårdh, 1931.
(syn.: *Trizerconoides* Jacot, 1938).
(Type: *Zercon ornatus* Träg., 1910 nec Berl., 1904 = *Zercon sarekensis* Willmann, 1939 = *Zercon radiatus* Berl., 1910).
3. Peritrematal shield with only two short setae (fig. 59); marginal setae of notogaster short, spinose; posterior depressions conspicuous. Similar in habitat to preceding genera *Prozercon* Sellnick in Willmann, 1943.
(Type: *Zercon fimbriatus* C. L. Koch, 1939).

* The genus *Seiodes* Berlese, 1887 (genotype: *Seiodes ursinus* Berl., 1887) is usually placed in this family, but as Evans (1955) has pointed out, its true systematic position must be considered uncertain pending a re-examination of the types.

MESOSTIGMATA-THINOZERCONOIDEA.

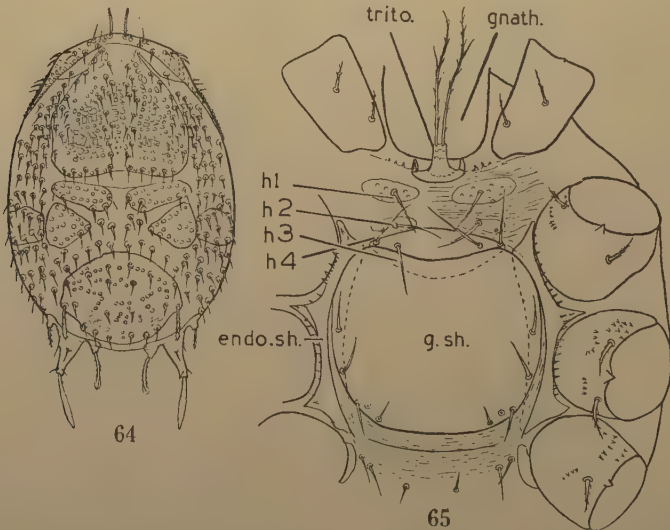
Only one thinozerconid has been recorded from the British Isles, namely, *Thinozercon michaeli* Halbert. The writer has not been able to examine this species which has been reported from a number of localities in Ireland. It appears to be restricted to the area between tide-marks on the seashore.

This group is characterized by the presence of praesternal setae flanking the tritosternum (fig. 63), the large jugularia, the form of the dorsal shields (fig. 62) and the position of the stigmata and peritremes.



FIGS. 62-63.—*Thinozercon michaeli* Halbert, ♀. Fig. 62, dorsum. Fig. 63, intercoxal region; (Based on Trägårdh, 1940).

g.sh., genital shield; h 1-h 4, sternal setae; jug., jugularia; per., peritreme; prae., praesternal seta; stig., stigmata; trito., tritosternum; v.sh., ventral shield.



FIGS. 64-65.—*Liroaspis togatus* (C. L. Koch), ♀. Fig. 64, dorsum. Fig. 65, intercoxal region. endo.sh., endopodal shield; gnath., gnathosoma; g.sh., genital shield; h 1-h 4, sternal setae; trito., tritosternum.

Family THINOZERCONIDAE Halbert, 1915.

THINOZERCONIDAE, Halbert, J. N. (1915). *Proc. Roy. Irish Acad.* 31, 8.

Genus THINOZERCON Halbert, 1915.

(Type: *Thinozercon michaeli* Halbt., 1915).

MESOSTIGMATA-LIROASPOIDEA.

The liroaspids are represented in the British fauna by only one species, *Liroaspis togatus* (C. L. Koch). The female is characterized by the form of the dorsal shields (fig. 64) and by the structure of the large genital shield (fig. 65). In the male the dorsum is covered by two shields of approximately equal size and the genital orifice, situated near the anterior margin of the sterniti-genital shield, is covered by a circular disc. In both sexes the stigmata and peritremes are ventro-lateral in position. The chelicerae are without processes and the *basis capituli* lacks the capitular setae. All legs are provided with claws. *L. togatus* occurs in humus and decaying wood.

Family LIROASPIDAE Trägårdh, 1946.

LIROASPIDAE, Trägårdh, I. (1946). *Lunds Universitets Arsskrift*. N.F. Avd. 2, 42, No. 4.

Genus LIROASPIS Banks, 1905.

(Syn. *Dwigubskyia* Oudemans, 1936).(Type: *Liroaspis americana* Banks, 1905).

MESOSTIGMATA-PROTODINCHOIDEA.

The Division Protodinychoidea is here proposed for a new species collected by Mr. M. E. Bacchus, Department of Entomology, British Museum (Nat. Hist.) from flood debris at Rydal Water, Westmorland. This species, female only, shows an affinity to the Parasitoidea in the form of the sternal region, genital shield and tritosternum whereas the gnathosoma, at least in the structure of the chelicerae and the arrangement of the rostral and posterior rostral setae, is of the type encountered in the Trachytoidea and Uropodoidea.

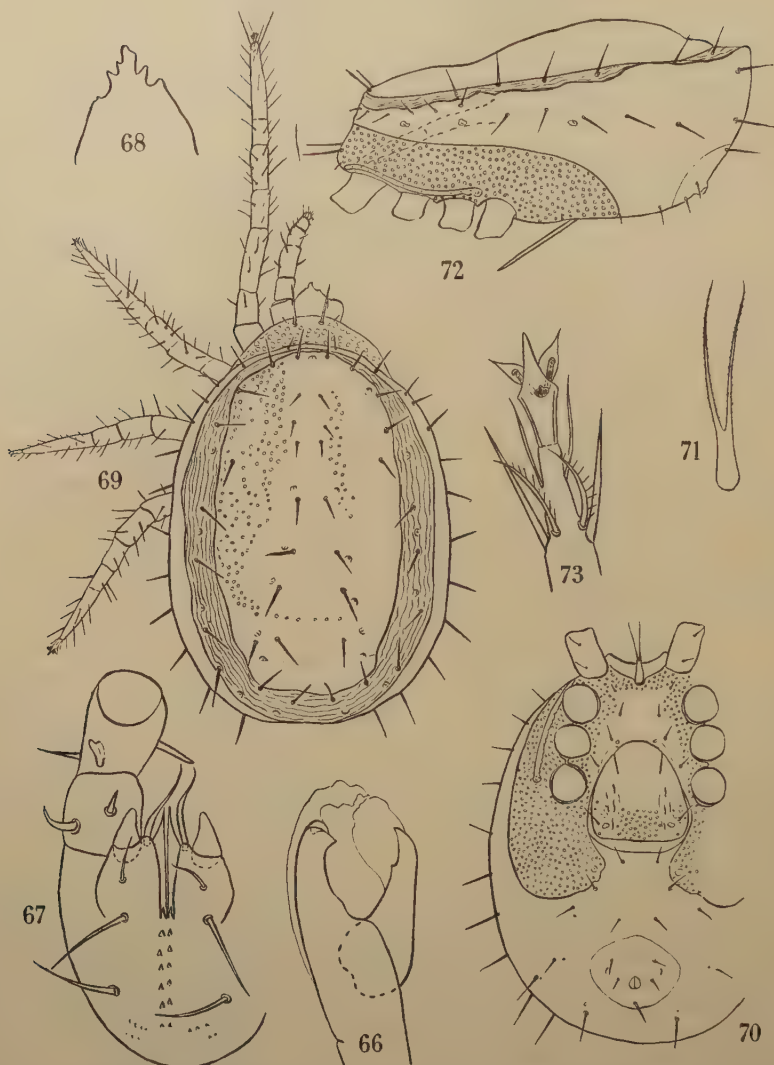
The gnathosoma is attached antero-ventrally to the idiosoma as in the parasitoids. The structure of the chelate chelicerae (fig. 66), the chaetotaxy of the *basis capituli* and rostrum (fig. 67), and the form of the tectum (fig. 68) are shown in the figures.

The idiosoma ($660\mu \times 520\mu$) is incompletely covered by a strongly sclerotized dorsal shield which is surrounded by a wide band of striated cuticle (fig. 69). The shield is provided with a number of stiff simple setae and pores. It is separated from the vertex shield anteriorly (fig. 70). The remainder of the body is sclerotized; the sternal-podal-peritrematal shield being strongly punctured and more heavily sclerotized than the rest (fig. 72). The tritosternum is bipartite (fig. 71) and widely separated from coxae I. Four pairs of sternal setae are present and the genital orifice is completely surrounded by a sclerotized shield and covered by a large uropodine-like genital shield provided with a pair of genital setae. The anal shield is more heavily sclerotized than the area surrounding it. The stigma is situated in the region of coxa IV with the peritreme extending beyond coxa I. The peritrematal shield is continuous anteriorly and forms the vertex which bears two pairs of setae. The legs are relatively long and each terminates in two claws and a three-lobed pulvillus (fig. 73).

Family PROTODINCHIDAE nov.

Genus *Protodinychus* nov.(Type: *Protodinychus punctatus*, sp. n.*).

* The Holotype ♀ (1955: 1: 11: 5), and the Paratype ♀ (1955: 1: 11: 6) are deposited in the British Museum (Nat. Hist.).



FIGS. 66-73.—*Protodinychus punctatus* ♀ gen. et sp. nov. Fig. 66, chelicera. Fig. 67, ventral view of gnathosoma. Fig. 68, tectum. Fig. 69, dorsum. Fig. 70, venter. Fig. 71, tritosternum. Fig. 72, lateral view. Fig. 73, ambulacral apparatus of leg II.
d.sh., dorsal shield; p.sh., peritrematal shield.

MESOSTIGMATA-TRACHYTOIDEA.

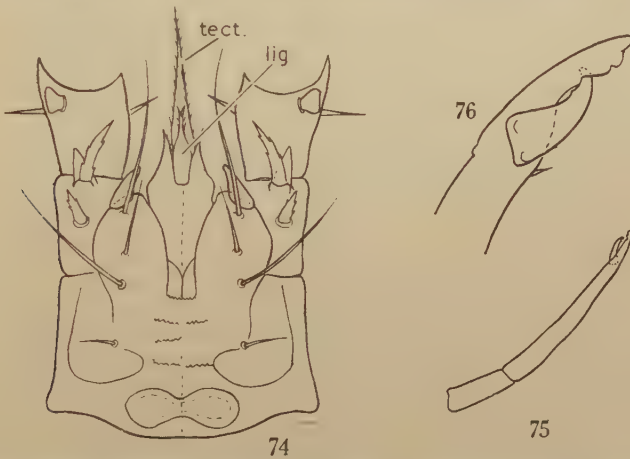
The Trachytoidea comprises a small group of mesostigmatid mites characterized by the structure of the tritosternum in the adult and immature stages, and the structure of the genital region in the female. The classification adopted in the present work follows that given by Camin (1953). The following details of the external morphology of members of this suborder refer to the Trachytidae which is the only family represented in the British fauna.

The gnathosomal setae are distributed as in the Protodinychoidea (fig. 74); the interior and exterior posterior rostrals are not paired as in the Parasitoidea (fig. 11). The corniculi are short and do not extend beyond the middle of the palpfemur. The pedipalp has five free segments. The chelicerae are long and uropodine-like. The fixed digit is considerably longer than the movable (fig. 76).

The dorsal surface is covered by a number of shields. The dorsal shield may be divided into an anterior and posterior shield and the lateral shields may be entire or fragmented. These shields are ornamented and, in the adult, may be covered with nymphal skins. The vertex is usually well-developed.

The tritosternum has a broad, rectangular base almost touching coxae I (fig. 2). The lacina is invariably branched. The region between coxae III and IV is almost entirely occupied by a large genital or epigynial shield without genital setae. The five pairs of intercoxal setae are shown in figs. 77 and 78. Trägårdh (1945) considers h 5 to be homologous with the metasternals of the Parasitoidea on the basis of each seta being associated with a 'pore' which he maintains is homologous with the third sternal 'pore' in the Parasitoidea. Setae h 4 are referred to as the pseudosternals. The metapodal shields are well-developed and cover the greater part of the region between the posterior margin of the genital shield and the ventri-anal shield.

The stigmata are situated ventro-laterally opposite coxae III. There are no depressions for the legs which are moderately long and all terminate in two claws.



FIGS. 74-76.—*Polyaspinus cylindricus* Berlese, ♀. Fig. 74, ventral view of gnathosoma. Fig. 75, chelicera. Fig. 76, fixed and movable digits of chelicera. lig., ligula; tect., tectum.

Family TRACHYTIDAE Trägårdh, 1938.

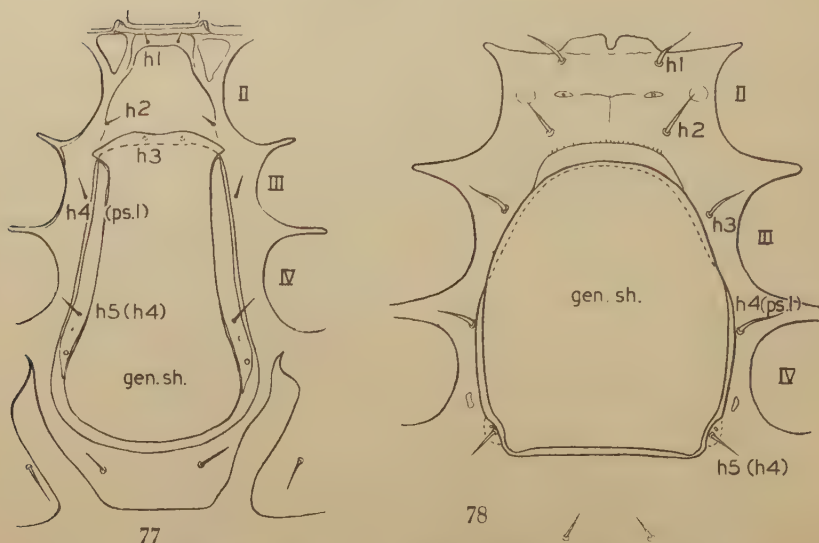
TRACHYTIDAE, Trägårdh, I. (1938). *Ent. Tidskr.* 59, 156.

The family *Trachytidae* contains, at present, only two genera,* *Trachytes* Michael and *Polyaspinus* Berlese. Both genera are represented in the British fauna. They occur in humus and decaying wood and are relatively common and widely distributed. The majority of the British species of *Trachytes* are keyed by Vitzthum (1931).

Key to genera.

1. Body elongate, parallel-sided, setae h 5 situated near the posterior corners of the large ovoid genital shield (fig. 78); marginal shields fragmented (marginal setae situated on small shields) *Polyaspinus* Berlese, 1916.
(Type: *Polyaspinus cylindricus* Berl., 1916).
- . Body broadly triangular in outline, vertex strongly developed; setae h 5 situated on large shields flanking a trapezoidal genital shield (fig. 77) *Trachytes* Michael, 1894.
(Type: *Celaeno aegrota* C. L. Koch, 1841).

* Turk (1953) also includes the genera *Neoseius* Oudemans, 1903 and *Uroseius* Berlese, 1888 in this family. Camin (1953), on the other hand, suggests they should be transferred, provisionally, to the *Uropodoidea*. The writer has not been able to examine specimens of the type species of these genera, and is forced at present to consider them, *genera incertae sedis*.



FIGS. 77-78.—Fig. 77, intercoxal region of *Trachytes minima* Trägårdh, ♀. Fig. 78, intercoxal region of *Polyaspinus cylindricus* Berlese, ♀.
gen.sh., genital shield; h 1-h 4, sternal setae; h 5, genital setae; ps.1, pseudosternal setae, II-IV, coxae II-IV.

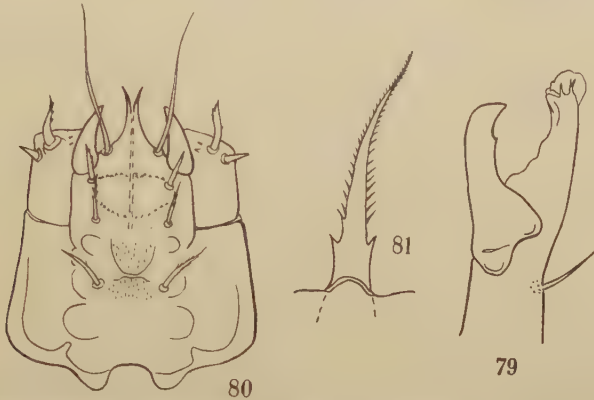
MESOSTIGMATA-UROPODOIDEA.

The uropodids are readily distinguished from other Mesostigmata by the presence of a camerostoma and the position of the tritosternum. They reach their maximum numbers and diversity of form in the tropical regions where they abound in decaying wood, humus, etc. The British representatives of this group are chiefly myrmecophilous in habit. The late nymphal stage in some species is frequently found attached to the exoskeleton of insects by an *anal stalk* or *pedicel* formed by an excretion from the anal region of the mite. This travelling stage is referred to as a *nympha pedunculata*.

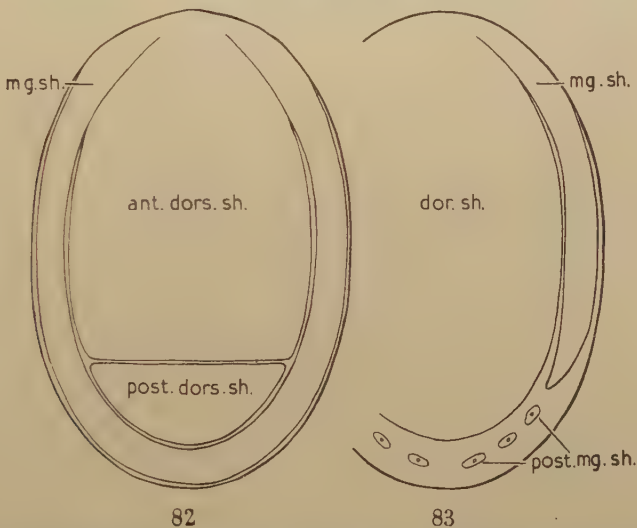
The *gnathosoma* is situated in a distinct cavity or camerostoma antero-ventrally (fig. 84). The roof of the camerostoma is formed by the body wall and its floor by the enlarged, trapezoidal coxae I. The shaft of the chelicera is usually much elongated with the digits chelate (fig. 79); the retracted chelicerae in some species extend almost to the posterior end of the body. The chelicerae are not modified in the male. The four pairs of setae on the *basis capituli-rostrum* are situated one behind the other and may be simple, pilose or serrated (fig. 80). The five free segments of the pedipalp are short and provided with simple or complex setae. Two or more setae situated on the palptarsus may be long and whip-like. The specialized palptarsal seta is two-pronged. The tectum is usually well-sclerotized and produced into a long denticulate process (fig. 81).

The *idiosoma*, generally strongly sclerotized in the adult stages, is oval in outline and often flattened. Its dorsal surface is covered by one or more shields—in British species a large dorsal shield surrounded by a marginal shield is usually present. The dorsal shield (*dors. sh.*) is rarely divided into an anterior (*ant. dors. sh.*) and posterior (*post. dors. sh.*) shield of unequal size (fig. 82). The marginal shield (*mg. sh.*), free, or fused with the dorsal and/or the ventral shields, may completely surround the lateral and posterior margins of the dorsal shield or may be reduced posteriorly so that region behind the dorsal shield is formed of striated cuticle provided with isolated *posterior marginal shields* or *scutellae* (fig. 83). Further, the marginal shield is sometimes differentiated into strongly sclerotized scutellae surrounded by weakly sclerotized cuticle (fig. 86). Both the dorsal and marginal shields are provided with

setae and pores. The *vertical setae* are often situated on a distinct *vertex shield* which is separated from the dorsal shield by a strip of cuticle. This shield may be strongly developed and act as a prow (Trägårdh, 1943 a).



FIGS. 79-81.—*Cilliba cassidea* (Hermann), ♀. Fig. 79, chelicera. Fig. 80, gnathosoma, ventral view. Fig. 81, tectum.



FIGS. 82-83.—Diagrammatic representation of the shields covering the dorsum in the UROPODOIDEA, ant.dors.sh., anterior dorsal shield; post.dors.sh., posterior dorsal shield; dor.sh., dorsal shield; mg.sh., marginal shield; post.mg.sh., posterior marginal shield.

The tritosternum lies in the camerostoma and is partially or completely covered by coxae I (fig. 3). The greater part of the venter in both sexes is completely covered by a compound shield formed by the fusion of the sternal, ventral and anal shields. This shield is smooth, punctured or reticulated. In some genera e.g. *Oplites* Berlese and *Oodinychus* Berlese, the anal shield is separated from the ventral shield by a distinct line or suture. The genital orifice in the female is enclosed in the sterniti-geniti-ventral shield and covered by a large well-sclerotized genital shield showing considerable variation in size and shape. In the male the aperture is circular or elongate-oval in outline and is located in the region of coxae II to IV. The ventral shield in both sexes may have a suture running from the middle of coxae IV to the lateral margin of the shield. This is termed a *metapodal line*.

The endopodal shields are fused with the sternal shield whereas the exopodals are developed into strong ridges separating one *leg groove* or *depression* from another.

The stigmata are situated in the region of coxae II to III with the peritreme usually strongly convoluted in adult stages. The legs are usually short with sclerotized ridges or protuberances on the femur and genu. Tarsus I is frequently without an ambulacral apparatus.

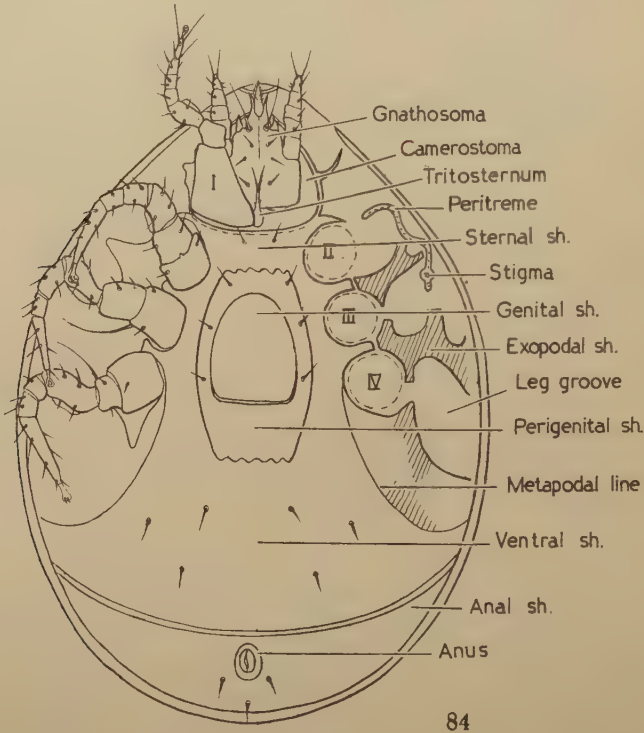


FIG. 84.—Ventral view of a uropodid mite (diagrammatic).

CLASSIFICATION.

The first comprehensive classification of the 'Uropodina' was proposed by Berlese (1918) in which the family *Uropodidae* was divided into the following tribes :

- | | |
|--|------------------|
| 1. Four stigmata, without peritremes | TREMATURINI. |
| 2. Two stigmata, peritremes present | 2. |
| 3. Tritosternum between coxae I | POLYASPIDINI. |
| 4. Tritosternum covered by coxae I | 3. |
| 5. Without depressions for the legs | PRODINYCHINI. |
| 6. With depressions for the legs | 4. |
| 7. Ventral surface covered by one shield which encloses the anal opening but is separated all round from the marginal shield | PHAULODINYCHINI. |
| 8. Ventral surface covered by one shield which is fused with the dorsal shield ; anal shield sometimes separate | 5. |
| 9. Inner border of the marginal shield strongly crenulate | URODINYCHINI. |
| 10. Inner border of the marginal shield weakly crenulate .. | 6. |
| 11. Shields very strongly sculptured, with deep pores or ridges .. | TRACHYUROPODINI. |
| 12. Shields smooth and polished | UROPODINI. |

This classification, with minor modifications, was adopted by Vitzthum (1929, 1931, 1940-1943). He transferred the Polyaspidini to the Sejina and elevated each tribe to family rank.

The characters used by Berlese to separate the Phaulodinychini, Urodinychini, Trachyuropodini and Uropodini are not sufficiently distinctive even for a practical classification of the group. The ornamentation of the dorsal and ventral shields

shows every gradation from the apparently smooth or minutely pitted shields of some Uropodini to the very heavily ornamented shields of some Trachyuropodini. Similarly, there is no definite distinction between those forms with a weakly crenulate inner border to the marginal shield and those with a strongly crenulate border. The obvious impracticability of this classification prompted Trägårdh (1944) to revise the family concept within the group using as his main characters the structure of the dorsal shield and the degree of fusion of the marginal shield with the dorsal and ventral shields. The following classification was the outcome of this investigation :

1. Anterior region of the marginal shields not fused with one another nor with the dorsal shield	TREMATURELLIDAE.
-. Anterior region of the marginal shields fused with one another	2.
2. Marginal shield completely surrounding the dorsal shield and separated from it by a suture	CILLIBIDAE.
-. Marginal shield fused with the anterior part of the dorsal shield	3.
3. Without depressions for the legs	4.
-. With depressions for the legs	5.
4. Well-defined postdorsal shield present	EUTRACHYTIDAE.
-. Without well-defined postdorsal shield	PRODINYCHIDAE.
5. Postdorsal shield present	URODIASPIDAE.
-. Postdorsal shield absent	6.
6. Marginal shield fused with the ventral shield	TRACHYUROPODIDAE.
-. Marginal shield fused with the dorsal shield	7.
7. Marginal shield reduced posteriorly	PHAULODINYOCHIDAE.
-. Marginal shield surrounding an entire dorsal shield	8.
8. Inner border of the marginal shield finely crenulate	URODINYCHIDAE.
-. Marginal shield not crenulate	UROPODIDAE.

The above classification, within the limits of the material examined by Trägårdh, undoubtedly shows an improvement on the earlier classification although the writer is doubtful of the validity of the families Cillibidae, Urodiaspidae and Urodinychidae. Neither of the two British species of the genus *Cilliba* (*minor* and *cassidea*) have the marginal shield *completely* separated from the dorsal shield by a suture; the shields showing a varying degree of fusion anteriorly. The separation of the Urodiaspidae on the basis of the division of the dorsal shield alone is unsatisfactory in the light of uropodid material examined by the writer from S. E. Asia and Africa—related species show varying degrees of separation of the dorsal shield into two parts. The retention of the family Urodinychidae is open to the same criticism as that given in the discussion of Berlese's classification.

Baker & Wharton (1951) have accepted Trägårdh's classification of the families of the Uropodina in its entirety but, at least in the Phaulodinychidae, Trachyuropodidae and Uropodidae, the arrangement of genera within the families follows that of Vitzthum (1940-1943) who based his classification on Berlese (1918). This results, for example, in the family Trachyuropodidae, characterized by the marginal shield being fused with the ventral shield, containing such genera as *Neodiscopoma* and *Olodiscus* in which the marginal shield is reduced posteriorly and not fused with the ventral shield. A classification of this nature is, to say the least, extremely misleading.

The writer has been unable to examine *spirit* material (mounted specimens are unsatisfactory) of a sufficient number of species in the Uropodidae and Trachyuropodidae to be certain of the correct assignment of genera to each family. Since the chief object of this work is to provide a guide to the identification of the British genera of the Mesostigmata the writer feels justified in lumping together, provisionally, these uropodids with depressions for the legs into one family, the Uropodidae.

Key to families.

- | | |
|--|------------------------|
| 1. Both sexes without depressions for the legs | PRODINYCHIDAE Berlese. |
| -. Both sexes with distinct depressions for the legs | UROPODIDAE Berlese. |

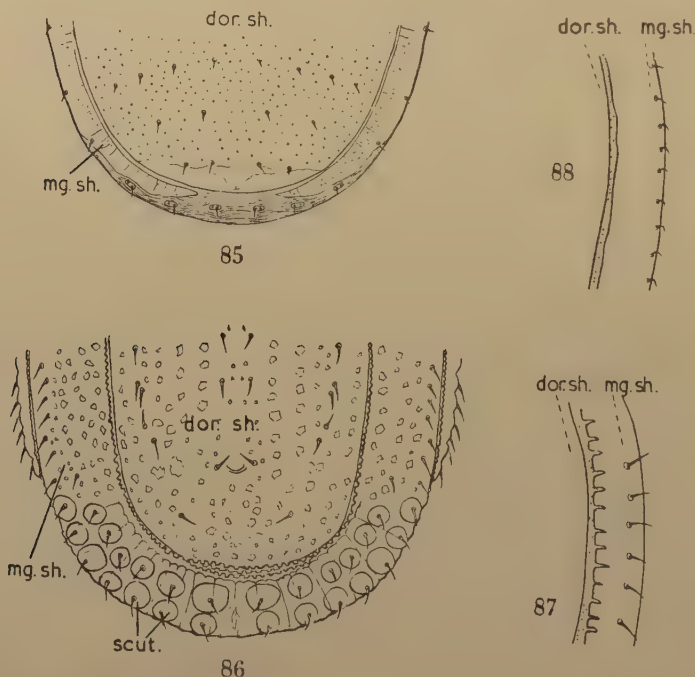
Family PRODINYCHIDAE Berlese, 1917.

PRODINYCHINI Berlese, A. (1918) [1917]*. *Redia*, 13, 9.

This family is represented in Britain by two genera. These are commonly encountered in decaying vegetation and moss. The separation of species in both genera is based chiefly on the shape of the peritreme (see Trägårdh, 1943, and Sellnick, 1945).

Key to genera.

1. Posterior region of the dorsal shield in both sexes with a transverse row of four strong pilose or serrated setae; marginal shield reduced posteriorly, region posterior to the dorsal shield occupied by a weakly sclerotized shield bearing four stout foliate setae covered with minute bristles *Dinychus* Kramer, 1882.
(syn. *Phyllodinychus* Trägårdh, 1943).
(Type: *Dinychus perforatus* Kramer, 1882).
- Posterior region of the dorsal shield without a transverse row of strong, pilose or serrated setae; marginal shield reduced posteriorly; region posterior to the dorsal shield with scutellae bearing simple setae *Prodinychus* Berlese, 1917.†
(syn. *Allodinychus* Trägårdh, 1943).
(Type: *Dinychus fimicola* Berlese, 1903).



FIGS. 85-88.—Fig. 85, postero-dorsal region of *Olodiscus minima* (Kramer). Fig. 86, postero-dorsal region of *Dinychura cordieri* (Berlese). Fig. 87, crenulate interior border of marginal shield in *Leiodychus krameri* (Canestrini). Fig. 88, smooth interior border of marginal shield in *Cilliba cassidea* (Hermann).
dor.sh., dorsal shield; mg.sh., marginal shield; scut., scutellae.

* Date of issue of separates !

† The generic name *Prodinychus* is first mentioned by Berlese in *Acarotheca Italica*, 1913, 3, but the type species was not designated until 1918 [1917] (*Redia*, 13, 9).

Family UROPODIDAE Berlese, 1913.

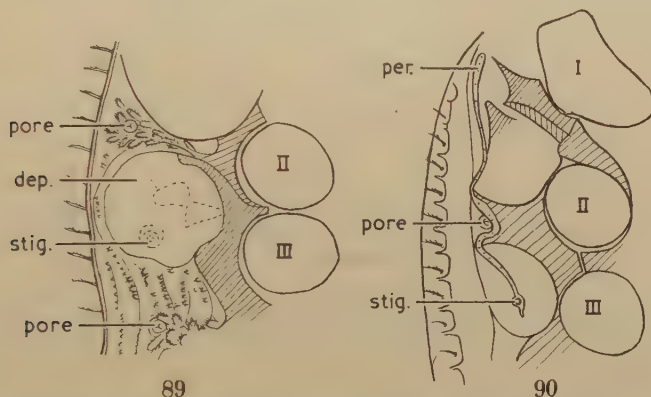
UROPODINI Berlese, A. (1913). *Acarotheca Italica* Firenze, 13.

The following key to the genera is based on the examination of British species only. The specimen should be thoroughly cleared in lactic acid before examination.

1. Tarsus I in both sexes without claws 2.
- Tarsus I both sexes with two claws 6.
2. Depressions for the legs shallow, poorly developed; marginal shield markedly reduced or absent; dorsal shield widely separated from the ventral shield; genital shield broadly oval in outline, produced into an acute spine anteriorly and reaching to the posterior margin of coxae II. In decaying vegetation *Phaulocylliba* Berlese, 1903.
(Type: *Phaulocylliba ventricosa* Berl., 1903).
- Depressions for the legs deeper, well-developed; marginal shield at least flanking part of the dorsal shield 3.
3. Marginal shield reduced posteriorly so that the region posterior to the dorsal shield is formed of striated cuticle with isolated scutellae (fig. 85) 4.
- Marginal shield continuous posteriorly and largely separate from the dorsal shield or completely fused with the dorsal shield so that the dorsum of the mite is covered by a single shield 5.
4. Small species, less than 500 μ in length; dorsal shield minutely punctured; genital shield elongate-oval and reaching to the middle of coxae II. Common in litter and humus *Olodiscus* Berlese, 1917.
(Type: *Discopoma integra* Berl., 1910 = *Uropoda minima* Kramer, 1882).
- Larger species, more than 700 μ in length; dorsal shield relatively heavily sculptured; genital shield reaching to the anterior margin of coxae III; genital orifice of male between coxae IV. In litter, humus, etc. *Neodiscopoma* Vitzthum, 1941.
(syn.: *Discopoma* Berl., 1904 nec Canestrini, 1882).
(Type: *Uropoda splendida* Kramer, 1882).
5. Body sub-circular; marginal shield distinct and continuous posteriorly, fused with ventral shield; dorsal and marginal setae relatively short; genital shield reaching to about the middle of coxae II; genital orifice of the male between coxae III and IV. Common in litter, humus, etc. *Cilliba* v. Heyden, 1826.
(Type: *Notaspis cassideus* Hermann, 1804).
- Dorsum covered by a single shield (? dorsal and marginal shields completely fused); dorsal setae relatively long, stiff; genital shield reaching to the middle of coxae II; genital orifice of the male between coxae III and IV. Mymecophilous *Trichocylliba* Berlese, 1903.
(Type: *Discopoma comata* Leonardi, 1895).
6. Marginal shield discontinuous posteriorly (cf. fig. 83) or differentiated into strongly sclerotized setae-bearing scutellae surrounded by weaker sclerotized cuticle (fig. 86) 7.
- Marginal shield apparently uniformly sclerotized and continuous posteriorly; inner border of marginal shield smooth or incised 11.
7. Marginal shield strongly reduced posteriorly, region posterior to dorsal shield formed of striated cuticle with isolated scutellae; dorsal shield entire or divided into an antero-dorsal and a postero-dorsal shield; genital shield extending to about the middle of coxae II; genital orifice of male between coxae III. In wrack on the seashore, in humus, etc. *Phaulodinychus* Berlese, 1903.
(syn.: *Halouropoda* Halbert, 1915 and *Phaulodiaspis* Vitzthum, 1925).
(Type: *Phaulodinychus repletus* Berlese, 1903 syn.: *Halouropoda interrupta* Halbert, 1915).
- Marginal shield differentiated into sclerotized setae-bearing shields, at least posterior to the dorsal shield.. 8.

8. Lateral and posterior portions of the marginal shield differentiated into scutellae; marginal setae inflated distally. Myrmecophilous *Uropolyaspis* Berlese, 1903.
(Type: *Uropoda hamulifera* Michael, 1894).
- Marginal shield differentiated into setae-bearing shields posteriorly only 9.
9. Dorsal shield heavily sculptured; scutellae large and numerous posteriorly (fig. 86); without metapodal lines. In humus, etc. *Dinychura* Berlese, 1913.
(Type: *Trachyuropoda* (*Urojanetia*) *rectangula* Berl., 1913).
- Dorsal shield less strongly sculptured; scutellae small and few posteriorly; with metapodal lines 10.
10. Anterior margin of the genital shield rounded and reaching to between coxae II and III; genital orifice in the male between coxae IV. In moss, under bark of trees, etc. *Urodinychus* Berlese, 1903.
(Type: *Uropoda carinata* Berl., 1888).
- Anterior margin of genital shield produced into an acute spine and reaching to coxae I; genital orifice of the male between coxae III. Myrmecophilous and in humus .. *Oodinychus* Berlese, 1917.
(Type: *Urodinychus janeti* Berl., 1904).
11. Adult stages without peritreme although present in the nymphae (figs. 89-90); genital shield truncated posteriorly, rounded anteriorly and reaching to the middle of coxae III; genital orifice of the male situated between coxae III. In floor dust in mills, etc. *Trematura* Berlese, 1917.
(Type: *Uropoda patavina* G. Canestrini, 1885).
- With peritremes in adult and nymphal stages (fig. 84). . 12.
12. Dorsal shield divided into a large antero-dorsal shield and a small postero-dorsal shield (cf. fig. 82); genital shield extending a short distance beyond the anterior margin of coxae II; genital orifice of the male between coxae III. Common in litter, humus, etc. *Urodiaspis* Berlese, 1916.
(Type: *Uropoda tecta* Kramer, 1876).
- Dorsal shield not divided into two distinct shields 13.
13. Both sexes with a perigenital shield (cf. fig. 84) 14.
- Both sexes without perigenital shield 15.
14. Anal and ventral shields completely fused; genital shield rounded anteriorly and reaching to the posterior margin of coxae II; genital orifice of male between coxae III and IV. Myrmecophilous *Urodiscella* Berlese, 1903.
(Type: *Uropoda ricasoliana* Berl., 1889).
- Anal and ventral shields separated by a well-defined line or suture; anterior margin of genital shield rounded and reaching to the middle of coxae II; genital orifice of male between coxae II and III. Myrmecophilous .. *Oplites* Berlese, 1884.
(syn.: *Uroplitella* Berl., 1904).
(Type: *Uropoda paradoxa* G. Canestrini & Berlese, 1884).
15. Without metapodal lines 16.
- With continuous metapodal lines 19.
16. Body, in both sexes, markedly constricted behind legs IV. Myrmecophilous *Leonardiella* Berlese, 1904.
(Type: *Uropoda canestriniana* Berl., 1891).
- Body not constricted behind legs IV 17.
17. Dorsal shield, behind legs IV, provided with a deep transverse groove with numerous stiff spine-like setae. Myrmecophilous *Trachyuropoda* Berlese, 1888.
(syn.: *Michaeliella* Berl., 1904).
(Type: *Trachyuropoda festiva* Berl., 1888).
- Dorsal shield without transverse groove behind legs IV. 18.
18. Dorsal and ventral shields not strongly ornamented; anal and ventral shields separated by a suture. Myrmecophilous *Uroobovella* Berlese, 1903.
(Type: *Uropoda obovata* G. Canestrini & Berlese, 1884).
- Dorsal and ventral shields heavily ornamented; anal and ventral shields fused; genital shield in the female reaching beyond coxae II; genital orifice of the male between coxae III. Myrmecophilous *Urotrachytes* Berlese, 1904, *s. lat.*

- (a) Anterior margin of the genital shield provided with a 'beard-like' hyaline extension *Urotrachytes* s. str.
(Type : *Uropoda formicariae* Lubbock, 1881).
- (b) Anterior margin of the genital shield without hyaline extension *Urojanetia* Berlese, 1913.
(syn. : *Janetiella* Berl., 1904 *nom. praeocc.*)
(Type : *Uropoda coccinea* Michael, 1891).
19. Inner border of the marginal shield strongly crenulate (fig. 87); genital shield very large and extending beyond the anterior margin of the sternal shield; genital orifice of the male between coxae II and III. In moss and decaying vegetable material *Leiodynchus* Berlese, 1917.
(Type : *Uropoda krameri* G. & R. Canestrini, 1882).
- Inner border of the marginal shield apparently smooth (cf. fig. 88) 20.
20. Posterior margin of the body with four long, whip-like setae. Associated with wood-boring beetles *Trichouropoda* Berlese, 1916.
(Type : *Uropoda longiseta* Berl., 1888).
- Posterior margin of the body without whip-like setae 21.
21. Body gently rounded posteriorly; marginal setae short, inconspicuous. In litter, humus, etc. *Pseudouropoda* Oudemans, 1936.
(syn. : *Notaspis* Koch, 1836 *nec* Hermann, 1804 and **Uropoda* Berl., 1917 *nec* Latreille, 1806).
(Type : *Acarus vegetans* Degeer, 1768).
- Body attenuated posteriorly; marginal setae relatively long, spine-like. In decaying vegetation *Fuscuropoda* Vitzthum, 1924.
(Type : *Notaspis marginatus* C. L. Koch, 1839).



FIGS. 89-90.—*Trematura jacksoni* Hughes. Fig. 89, position of the stigma in the female. Fig. 90, position of the stigma and peritreme in the deutonymph.
dep., depression for leg; per., peritreme; stig., stigma; I-III, coxae of legs I-III.

MESOSTIGMATA-FEDRIZZIOIDEA.

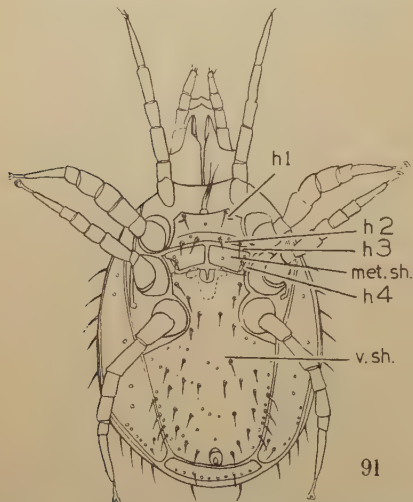
In the present work Trägårdh's concept of the cohort Fedrizzina is modified to include his Celaenopsina. The fedrizzids are characterized chiefly by the structure of the shields covering the genital orifice in the female. In the other groups treated in this work the female genital orifice is covered by a single shield (except in some weakly sclerotized parasitic forms where it is lacking), whereas in the present group the orifice is covered by three shields, the genital and the paired laterals. Throughout the group these shields show considerable variation in form either through reduction in size or coalescence (cf. fig. 91). Further characteristics of this group are the absence of an ambulacral apparatus on leg I and the presence of

* The genus *Uropoda* Latreille, 1806 (type : *Acarus vegetans* Latreille, 1806 (?) = *Acarus orbicularis* Müller, 1776) is omitted from the above key because it is known from immature stages only. The deutonymph, commonly found on dung inhabiting insects, lacks an ambulacral apparatus on leg I.

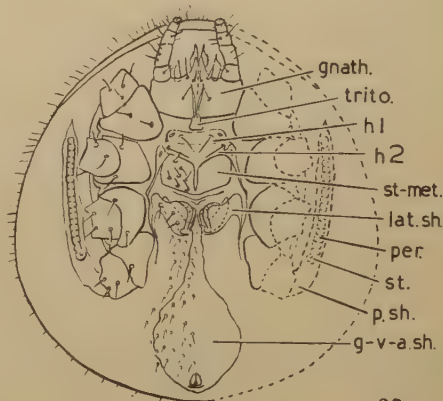
variously formed processes from one or both digits of the chelicera. The fedrizzids are normally found in association with insects or other arthropods.

Only two genera have been recorded from Britain. These belong to two families which may be separated as follows :

1. Without a genital shield ; lateral shields completely fused with each other except for a small indentation anteriorly (fig. 91), genital orifice of male praesternal..... CELAENOPSIDAE Berlese.
- . Genital shield present ; lateral shields distinct (fig. 92), genital orifice of male in the region of coxae III..... ANTENNOPHORIDAE Berlese.



91



92

FIG. 91.—*Celaenopsis badius* (C. L. Koch), venter of female (based on Vitzthum, 1931).
h 1–h 4, sternal setae ; met.sh., metasternal shield ; v.sh., ventral shield.

FIG. 92.—Ventral view of *Antennophorus* sp.

gnath., gnathosoma ; g.-v.-a.sh., geniti-ventri-anal shield ; h 1–h 2, sternal setae 1–2 ; lat.sh., lateral shield ; per., peritreme ; p.sh., peritrematal shield ; st., stigma ; st.-met., sterniti-metasternal shield ; trito., tritosternum.

Family CELAENOPSIDAE Berlese, 1892.

CELAENOPSIDAE, Berlese, A. (1892). *Acari Myriopoda et Scorpiones*. . . (Ordo Mesostigmata), 15.

The only British species of this family, *Celaenopsis badius* (C. L. Koch), occurs under bark of trees and in moss.

Genus *Celaenopsis* Berlese, 1886.

(syn. *Antennocelaeno* Berl., 1903).

(Type : *Gamasus cuspidatus* Kramer, 1876 = *Gamasus badius* C. L. Koch, 1839).

Family ANTENNOPHORIDAE Berlese, 1892.

ANTENNOPHORIDAE Berlese, A. (1892). *Acari Myriopoda et Scorpiones*. . . (Ordo Mesostigmata), 15.

Represented in Britain by the myrmecophilous genus *Antennophorus* only.

Genus *Antennophorus* Haller, 1887.

(Type : *Antennophorus uhlmanni* Haller, 1887).

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I am extremely grateful to my colleague Mr. E. Browning, for his invaluable assistance with the preparation of this work, and to Dr. H. W. Parker for reading the manuscript.

GLOSSARY.

(Numbers in the brackets refer to figures in the text.)

- Ambulacral apparatus** : The claws and pulvillus of an ambulatory appendage. (4, 43 and 57.)
Ambulatory appendages : The appendages of segments III-VI used primarily for walking.
Anal shield : A sclerotized shield surrounding the anus and provided with three setae (the para-anals and the post-anal seta) except in species showing increased setation of the dorsal and ventral shields e.g. *Haemogamasus* Berl. (34 and 47.)
Antero-dorsal shield : In the case of the division of the dorsal shield into two parts, the anterior shield is referred to as the antero-dorsal shield or notocephale. (25 and 60.)
Axillary process : An accessory process or spur associated with the large spur on the femur of leg II in some Gamasina. (30.)
Basi-femur : The proximal segment resulting from the partial or complete division of the femur of an ambulatory appendage.
Basis capituli : A sclerotized tube enclosing the chelicerae ; its dorsal wall formed by the tectum and its lateral and ventral walls formed by the coxae of the pedipalps. (41 and 69.)
Camerostoma : A cavity situated antero-ventrally in the Uropodina in which the gnathosoma is situated. (84.)
Capitular groove : A groove associated with the hypostome and usually provided with rows of denticles. (40 and 41.)
Capitular setae : Paired setae, one on either side of the capitular groove, associated with the *basis capituli*. These setae are absent in the larva. (11.)
Chelate : Opposing digits of the chelicerae forming a pincer-like structure.
Chelate-dentate : Digits of a chelate appendage provided with teeth. (5.)
Chelicerae : The first pair of appendages (pre-oral) in the Arachnida which are modified for feeding. (4.)
Corniculi : Paired horn-like structures associated with the rostrum. (40 and 41.)
Coxa : The basal segment of the pedipalps and ambulatory appendages. (1.)
Crassate : Term used to describe the enlarged or swollen segments of leg II in some males of the Gamasina. (30.)
Deutonymph : The third post-embryonic developmental stage in the life-cycle. This stage has eight legs.
Dorsal series : A longitudinal row of setae situated medially on the dorsal shield. (37-39.)
Dorsal shield : A sclerotized shield partially or completely covering the dorsum of adult and some immature stages. (22.)
Endopodal shield : A sclerotized shield or plate associated with the inner margin of the coxae of the legs. (1.)
Epigynial shield : Same as Genital shield.
Epistome : Same as Tectum.
Exopodal shield : A sclerotized shield or plate associated with the outer margin of the coxae of the legs. (1.)
Femur : A segment of the pedipalps and legs situated between the trochanter and genu. (1 and 19.)
Fixed digit : The immovable distal part of the second segment of the chelicerae. (5 and 7.)
Genital setae : Paired setae situated on or in close proximity to a sclerotized genital shield. (1.)
Genital shield : A sclerotized shield covering the genital orifice in the females. It may be provided with an anterior hyaline extension which functions as a chute during oviposition. (1, 7.)
Geniti-ventral shield : The compound shield, bearing more than one pair of setae, formed by the fusion of the genital shield with part of the ventral shield.
Genu : A segment of the pedipalp and legs situated between the femur and tibia. (4.)
Gnathosoma : A tubular sclerotized structure, formed by the first (chelicerae) and second (pedipalps) pair of appendages, attached antero-ventrally to the idiosoma. (4.)
Holovertral shield : A compound shield formed by the fusion of the sternal, genital, ventral and anal shields. (48.)
Hypostome : Part of the gnathosoma separating, ventrally, the coxae of the pedipalps.
Idiosoma : That part of the body of the mite excluding the gnathosoma. (84.)
Internal trochanter seta : The seta situated on the internal surface of the trochanter of the pedipalp. (40 and 41.)
Interseutal membrane : Smooth, striated or granular cuticle connecting the sclerotized shields. (38 and 39.)

- Jugular shields (Jugularia):** A pair of shields bearing the first sternal setae and situated in the region of coxae I-II. (4.)
- Lacinae:** Smooth or pilose branches of the tritosternum. (1.)
- Larva:** The first post-embryonic stage in the development of the Acarina and provided with only six legs.
- Lateral shields:** A pair of shields bearing setae, flanking the genital shield and lying between it and the sternal shield. (92.)
- Leg grooves:** Depressions or grooves situated between coxae II-IV and the margin of the body into which the legs can be withdrawn. These depressions are present only in some groups of the Uropodoidea. (84.)
- Lyriform organ:** Elongate pore-like structures located on the chelicerae and the sternal shield. (5.)
- Marginal series:** The external longitudinal row of setae on the dorsal shield in the Parasitoidea. (38.)
- Marginal shield:** A sclerotized shield partially or completely surrounding the dorsal shield; sometimes in the form of isolated setae-bearing scutellae. (82 and 83.)
- Metapodal line:** A distinct line or suture extending from coxae IV to the lateral margin of the ventral shield in some Uropodoidea. (84.)
- Metapodal shields:** One or more shields situated posterior to coxae IV. (4.) These are sometimes fused with the peritrematal shield.
- Metasternal setae:** The fourth pair of sternal setae (h 4) situated on the sternal shield on the metasternal shields or on the interscutal membrane. (4 and 28.)
- Metatarsus:** The proximal segment resulting from the division of the tarsus of the legs. (4.)
- Movable digit:** The ultimate segment of the chelicera situated ventro-laterally to the fixed digit. (4-8.)
- Mycetophilous:** Feeding on fungi.
- Myrmecophilous:** Associated with ants (Hymenoptera).
- Notocephale:** Same as antero-dorsal shield.
- Notogaster:** Same as postero-dorsal shield.
- Nympha coleoptrata:** The deutonymphal stage of some parasitids found on beetles which they use as a means of transportation.
- Nympha pedunculata:** The deutonymphal (?) stage of some Uropodoidea attached by an anal stalk or peduncle to insects, etc.
- Palptarsal seta:** A specialized pronged seta situated ventro-laterally on the interior margin of the tarsus of the pedipalp.
- Para-anal setae:** A pair of setae situated in the region of the anus. (4.)
- Para-podal shields:** Same as exo-podal shields.
- Para-sternal shields:** A pair of shields situated between the metasternal and genital shields in the Paresitidae. These shields may be homologous with the lateral shields. (28.)
- Pedipalps:** The first pair of post-oral appendages; its free segments being chiefly sensory in function. (4, 18 and 19.)
- Perigenital shield:** A well-defined shield-like area surrounding the genital shield of the female and the genital orifice of the male in some Uropodoidea. (84.)
- Peritrematal shield:** The shield enclosing the stigma and peritreme. (44.)
- Peritreme (Peritrema):** A sclerotized tube-like structure extending anteriorly, and sometimes posteriorly, from the stigma. (4 and 44.)
- Pilus dentarius:** Same as *Pilus dentilis*.
- Pilus dentilis:** A seta-like organ, probably sensory in function, situated on the fixed digits of the chelicerae. (49 and 50.)
- Post-anal seta:** A single seta situated posterior to the anus (4.)
- Posterior marginal shield:** A shield derived from the marginal shield and situated posterior to the dorsal shield. (83.)
- Posterior rostral setae:** One (in the larva) or two pairs (in the nymphal and adult stages) of setae situated posterior to the rostral setae. (11.)
- Postero-dorsal shield:** In the case of the division of the dorsal shield into two parts, the posterior shield is referred to as the postero-dorsal shield or notogaster. (82.)
- Prae-endopodal shields:** One or more pairs of small shields *without setae* situated anterior to the sternal shield. (4.)
- Praesternal setae:** A pair of setae situated one on either side of the tritosternum in some groups e.g. Thinozerconioidea.
- Prae-tarsus:** The ultimate segment of the leg bearing the ambulacral apparatus. (4.)
- Pre-anal setae:** Setae situated anterior to the para-anal setae on the ventri-anal shield and indicating the fusion of the anal and ventral shields. (4.)
- Protonymph:** The second post-embryonic development stage in the life cycle of most Acarina. This stage has eight legs.
- Pseudosternal setae:** A pair of setae situated in the intercoxal region of the Trachytoidea. (77 and 78.)
- Pulvillus:** A lobate, hyaline structure associated with the claws of the legs. (42 and 43.)
- Rostral setae:** A pair of setae located anteriorly on the rostrum. These are present in all post-embryonic developmental stages of non-specialized Mesostigmata. (11.)
- Rostrum:** A beak-like structure of the gnathosoma. (11 and 12.)
- Scutellae:** Small shields.

- Spermatophoral process**: A simple or complicated process arising from the proximal half of the movable digit of the chelicerae in males of the Parasitoidea. It functions as an accessory copulatory organ. (6 and 7.)
- Sternal pores**: Pore-like structures associated with the sternal setae. (33.)
- Sternal setae**: Four pairs of setae usually situated on a sclerotized shield in the intercoxal region. (4 and 33.)
- Sternal shield**: A shield resulting from the fusion of the coxal shields of legs I-IV. (4.)
- Sterniti-genital shield**: A compound shield formed by the fusion of the sternal and genital shield in the male. (55.)
- Sterniti-geniti-ventral shield**: A compound shield formed by the fusion of the sternal, genital and ventral shields in the male. (48.)
- Stigma**: An opening of the respiratory system situated in the region of coxae II-IV either ventrally, ventro-laterally or dorso-laterally. (4.)
- Tarsus**: The terminal segment of the pedipalp and also of the leg when the prae-tarsus is absent. (4.)
- Tectum**: The tectum forms the dorsal wall of the gnathosoma and is produced anteriorly to roof the rostrum. Its anterior margin is often produced into simple or complex processes. (12-17.)
- Telo-femur**: The distal segment resulting from the partial or complete division of the femur of the legs.
- Tibia**: The segment of the pedipalp or leg lying between the genu and tarsus. (4.)
- Tritosternum**: The remnant of the sternite of the third segment. This is usually situated posterior to the gnathosoma and between or under coxae I. (1-3.)
- Trochanter**: The segment situated between the coxa and femur of the legs and pedipalps. (4.)
- Vaginal sclerites**: Plates formed by the sclerotization of the wall of the vagina.
- Ventral groove**: Same as Capitular groove.
- Ventri-anal shield**: A compound shield resulting from the fusion of the anal and ventral shields and characterized by bearing pre-anal setae. (4, 45 and 46.)
- Vertex**: The sclerotized antero-dorsal region of the idiosoma, usually bearing the vertical setae.
- Vertex shield**: The shield bearing the vertical setae. This shield may be fused with or separated from the dorsal shield.
- Vertical setae**: A pair of setae situated on the anterior margin of the dorsal shield or on the vertex shield. These setae often differ in structure from other dorsal setae.

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* The date in the squared brackets refers to the date of issue of separates of this work and is therefore the date of publication of new species, etc.

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THE MESOZOIC FISSURES OF THE BRISTOL CHANNEL AREA AND THEIR VERTEBRATE FAUNAS. By PAMELA LAMPLUGH ROBINSON, B.Sc., Department of Zoology, University College, London. (Communicated by Professor P. B. MEDAWAR, F.R.S., F.L.S.)

(With Plates 1 to 4 and 6 text-figures.)

[Read 19 January 1956.]

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INTRODUCTION.

Mesozoic deposits occurring as fissure fillings in the Carboniferous Limestone of the Bristol Channel area (Somerset, South Gloucestershire, Glamorgan) have provided a rich yield of a great variety of terrestrial vertebrates that fall into two groups. One, which consists mainly of mammals and mammal-like reptiles, is Rhaetic or Lower Liassic in age, and is found in fissures of submarine origin. The other group contains sauropsid reptiles only, occurring in a matrix which may be red, green, or yellow in colour and is devoid of marine invertebrates. It has been suggested that the latter group is Triassic in age, possibly Keuper.

Most of the Rhaetic and Liassic terrestrial vertebrates found in this area have already been described (Owen, 1871; Simpson, 1928; Parrington, 1941, 1946; Kühne, 1949, 1950). Kühne has described two of the submarine fissures, one Rhaetic and one Liassic, in which he found his fossil material. The Triassic reptiles await description, and their study will necessarily take several years. The fissures in which these latter reptiles are found have not been described; they are quite different in origin and history from those of Rhaetic and Liassic age. No evidence has ever been given for the age assigned to the Triassic fissure deposits, and on theoretical grounds they could be of any age post-Carboniferous but pre-Rhaetic.

This paper is intended to serve as a background to the descriptions of the various Triassic reptiles from fissure localities in the Bristol Channel area. After a brief description of their mode of origin and infilling the age of the fissure deposits is

discussed and the probable physical conditions which obtained at the time outlined. A preliminary discussion of the whole of this Triassic fauna, and its significance, follows.

HISTORY OF RESEARCH.

Charles Moore was a very active worker in the Bristol Channel area during the nineteenth century. He was the first to recognize and examine systematically certain deposits of Rhaetic and Liassic age occurring as fillings in fissures in the Carboniferous Limestone near Frome and Bristol (Moore, 1867, 1881). His best known work was the discovery of twenty-nine mammalian teeth in a Rhaetic fissure near Holwell (Owen, 1871; Simpson, 1928).

Mr. F. G. Hudson was the first to discover a fossiliferous fissure of non-marine origin. It was found in the Carboniferous Limestone at Slickstones Quarry, near Cromhall, Gloucestershire, in 1938. A few pieces of the material were sent to the British Museum. They were briefly described by Dr. W. E. Swinton (1939), who gave the name *Gleirosaurus hudsoni* to jaws which appeared to be rhynchocephalian. The bulk of the material, still undescribed, is in the possession of Professor W. F. Whittard at Bristol.

Dr. W. G. Kühne came to England from Germany in 1939, with a particular interest in Mesozoic mammals. The known material of Jurassic mammals consisted mainly of teeth and jaws. Kühne sought new and more adequate material, in order to gain a better knowledge of mammalian evolution during Jurassic times. He knew that a part of the Mendip Hills had remained a land area, as a series of islands, in Rhaetic and early Jurassic times, that Moore had found mammalian teeth in a submarine Rhaetic fissure in the area, and that a number of other fissures had been described by Moore. The fissures had all occurred in Carboniferous Limestone, and exposures of the Limestone were numerous in quarries and as natural outcrops. On the basis of this knowledge, and realizing that no one had studied the Mendip fissures since Moore died in 1881, Kühne commenced a systematic search for fossiliferous fissure-deposits in the Mendip area.

At Holwell, in Moore's 'Microlestes' quarry (fig. 1), he found twenty mammalian teeth in a fissure-filling (Kühne, 1946; Parrington, 1941, 1946). Most of these teeth were Microleptids, but two were Triconodonts, the oldest record of the group then known. Near Shepton Mallet, at Windsor Hill Quarry (fig. 1), he discovered a fissure of Lower Liassic age containing abundant bones of *Oligokyphus*, previously known only from teeth, and has been able to write a fairly complete osteology of the whole animal. In 1946, at Emborough Quarry, Old Down, about six miles N.N.E. of Wells (fig. 1), he found a Triassic fissure deposit containing a great quantity of well preserved but dissociated small reptile bones. In the same year, at Batscombe, near Cheddar (fig. 1), he collected small reptile bones, similar to those found at Emborough Quarry, from another very fossiliferous Triassic fissure deposit. He also found one small fragmentary reptile jaw in another Triassic fissure at Highercoft Quarry near Gurney Slade (fig. 1).

Kühne next turned his attention to South Wales. The geological history of Glamorgan in Triassic, Rhaetic and early Jurassic times is rather similar to that of the Mendip Hills of Somerset. In Glamorgan there were considerable outcrops of Carboniferous Limestone, which remained partly above water as islands in Rhaetic times, and were not submerged until the *bucklandi* zone of the Lower Lias (Trueman, 1922). Here he began to search the numerous quarries for fossiliferous fissure deposits. Unknown to Kühne, Mr. Trevor M. Thomas and his brother had discovered a fossiliferous Triassic fissure deposit at Ruthin Quarry, St. Mary Hill, near Cowbridge (fig. 1). This locality has since been described by Mr. Thomas (1952), and a quantity of the material collected has been presented to the National Museum of Wales, Cardiff. Kühne also found this locality and collected a small amount of material which is now in the British Museum (Natural History). At Duchy Quarry, between Southerndown Road Station and Ewenny, south of Bridgend (fig. 1), Kühne discovered a small quantity of matrix which had been part of a fissure-filling. The fissure itself

had at that time been quarried away. The matrix yielded about fifty teeth, or fragments of teeth. The fauna consists mainly of Triconodonts, almost identical with those found by Professor Peyer in the Upper Rhaetic of Hallau. One tooth proved to be that of a Symmetrodont, and is the oldest known record of this group (Kühne, 1949, 1950).

Dr. Kühne returned to Germany in 1951. Continuing his work in the field, I found a new Triassic fissure deposit at Slickstones Quarry, near Cromhall in Gloucestershire in 1951, from which a fauna of small reptiles has been collected (Robinson, Kermack and Joysey, 1951). In 1952 my colleague Dr. K. A. Kermack joined in the hunt, and we discovered bone-rich material containing at least five different reptiles at Pant-y-ffynon Quarry, near Cowbridge, Glamorgan. This locality was the first to yield associated bones.

In his paper in 1946, Dr. Kühne emphasized "... the desirability of strict surveillance of all quarries in the Carboniferous Limestone of Somerset and South Glamorgan. As quarrying continues, new fissures may be revealed at any time". These words have been fully confirmed by the experience of Dr. Kermack and myself.

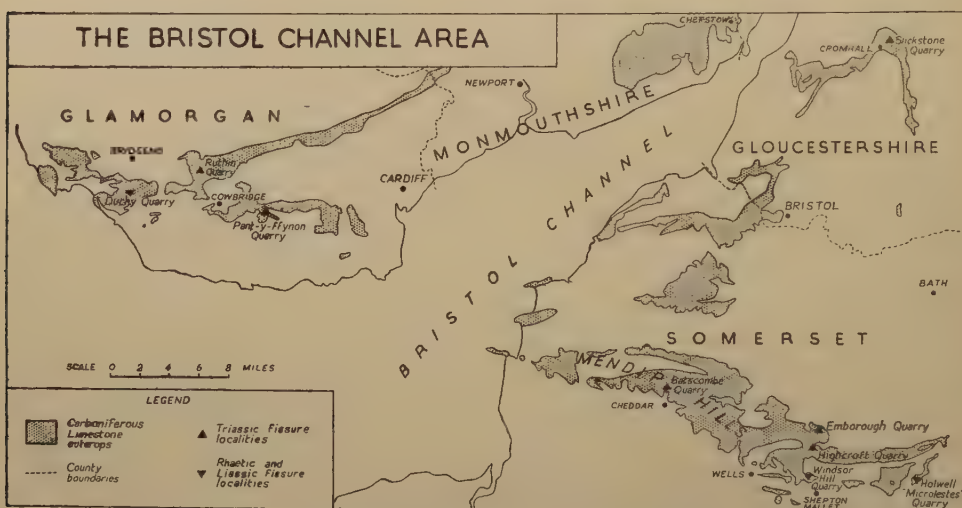


FIG. 1.—The Mesozoic fissure localities of the Bristol Channel area.

The fossiliferous material from Pant-y-ffynon Quarry was found on the tip. No trace remained of the fissure which had housed it. Another winter's exposure to the weather would have resulted in complete disintegration of the material. Yet the fissure had appeared since Kühne had searched the quarry a few years previously. In future all limestone quarries in work in the Bristol Channel area will be inspected annually, those in South Wales by Dr. Kermack, and those in Somerset and Gloucestershire by myself.

In Table I all the fissure localities of the Bristol Channel area which have yielded terrestrial vertebrates are listed, together with their contents as far as is known at present. Three localities have yielded nine species of mammals or mammal-like forms of Rhaetic or Liassic age. Six localities have yielded about nineteen different species of reptiles of Triassic age. The reptile fauna of Durdham Down, Bristol (*Thecodontosaurus antiquus* Morris, *T. platyodon* (Riley & Stutchbury), and *Palaeosaurus cylindron* (Riley & Stutchbury) has been omitted from the list as the fossils seem to have been found in a depression in the Palaeozoic land surface and not in a fissure (Riley & Stutchbury, 1840; Etheridge, 1870).

TABLE I.
TERRESTRIAL VERTEBRATES FROM FISSURES IN THE BRISTOL CHANNEL AREA

Windsor Hill Quarry, near Shepton Mallet, Somerset.	{ <i>Oligokyphus major</i> Kühne <i>Oligokyphus minor</i> Kühne }	about 2,000 specimens, dissociated	} Lower Lias (Charmouthian)	1939 W. G. Kühne
Duchy Quarry, near Southendown Road Station, Glamorgan	{ <i>Morganicodon watsoni</i> Kühne Other Triconodont teeth A Symmetrodont }	1 specimen about 50 specimens 1 specimen	} Rhaeto-Liassic	1947 W. G. Kühne
Holwell Southern ('Microlestes') Quarry, Near Frome, Somerset	{ <i>Microcleptes moorei</i> (Owen) <i>Microcleptes fissurae</i> Simpson <i>Thomastia anglica</i> Simpson ? Microleptid iraisors or canines Reptiles <i>Eozostrodon parvus</i> Parrington <i>Eozostrodon problematicus</i> Parrington Microleptid teeth Incisors or canines Placodont teeth Crocodilian teeth }	9 specimens 3 specimens 3 specimens 5 specimens unidentified fragments 1 specimen 1 specimen 13 specimens 5 specimens a few specimens a few specimens	originally 29 specimens } Rhaetic } Rhaetic	circa 1860 C. Moore 1939 W. G. Kühne
Slickstones Quarry, near Cromhall, Gloucestershire	{ <i>Glevosaurus hudsoni</i> Swinton* About 9 species of reptiles }		Triassic Triassic	1938 F. G. Hudson 1951 P. L. Robinson
Emborough Quarry, Old Down, near Wells, Somerset	{ A lepidosaur An archosaur 2 other reptiles }	abundant specimens a few specimens rare	} Triassic	1946 W. G. Kühne
Batscombe Quarry, near Cheddar, Somerset	The Emborough lepidosaur	abundant	Triassic	1946 W. G. Kühne
Highcroft Quarry, near Gurney Slade, Somerset	A reptile jaw	one fragment	Triassic	1946 W. G. Kühne
Ruthin Quarry, St. Mary Hill, nr. Cowbridge, Glamorgan	A reptile (jaws)	abundant, fragmentary	Triassic	T. M. Thomas
Pant-y-ffynon Quarry, near Bonvilston, Glamorgan	Five reptiles	abundant	Triassic	1952 { K. A. Kernack P. L. Robinson

* Generic name published as *Clevosaurus* due to a typographical error.

FISSURES.

The term fissure is a compendious one: yet it is convenient to retain it to refer to a number of phenomena which have in common the fact that they consist of relatively small quantities of younger deposits found enclosed in rocks of an earlier age. In the Bristol Channel area there are several different kinds of fissure; only one of these, of submarine origin, has been described previously (Moore, 1867, 1881; Kühne, 1946). This paper is mainly concerned with another type of fissure, of terrestrial origin, in which pre-Rhaetic vertebrates have been found; but a brief description of three other types will be given.

Fissures are small-scale phenomena, but their formation is invariably closely connected with the general geological history of the areas in which they are found. A brief description of the relevant part of the geological history of the Bristol Channel area is a necessary preliminary to a discussion of the fissures which occur there. For the sake of brevity it is convenient to select a part of the area, the Mendip Hills of Somerset, for detailed examination and to serve, in general terms, as an illustration of the whole.

THE GEOLOGY OF THE MENDIP AREA OF SOMERSET.

The geological formations in the Mendip area are:—

MESOZOIC	{	Jurassic	{ Great Oolite Inferior Oolite Lias Rhaetic
		Triassic	Dolomitic conglomerate and red marls and sandstones
PALAEOZOIC	{	? Permian	Sandstones and conglomerate
		Carboniferous	{ Coal Measures Grits Limestone
		Devonian	Upper Old Red Sandstone
		Silurian	{ Wenlock mudstones and pyroxene andesites Llandovery tuffs and lava.

At the end of the Carboniferous period the Palaeozoic rocks of the Mendip area were folded into four periclinal, each with its long axis running east-west, arranged *en echelon* along a line running west-north-west—east-south-east (fig. 2). Fracturing and thrusting accompanied the folding (Welch, 1929, 1933). During the Permian and Trias the area was part of a continent on which the four folds formed a structurally controlled ridge, the Triassic Mendip Hills. To the south of these hills a depression stretched as far as the highlands of Devon and West Somerset. This southern depression slowly sagged during Triassic times, so allowing a considerable thickness of terrestrial sediments to accumulate in it. At Puriton, west-north-west of Compton Dundon, borehole records show 1,250 feet of Upper Triassic marls and saline deposits, and below these nearly 800 feet of Lower Triassic and ? Permian sandstones and conglomerate, yet the base of the Permo-Triassic rocks was not reached. To the north of the Triassic Mendip Hills was an area occupied by a synclinal basin of Coal Measures, the Bristol Coalfields. The preservation of the Coal Measures in this synclinal basin shows that comparatively little erosion occurred there during Permo-Triassic times, and the region was one of low relief. Yet the Triassic sediments are thin, the maximum thickness being about 200 feet. These characters suggest that during Triassic time the Bristol Coalfield area was more

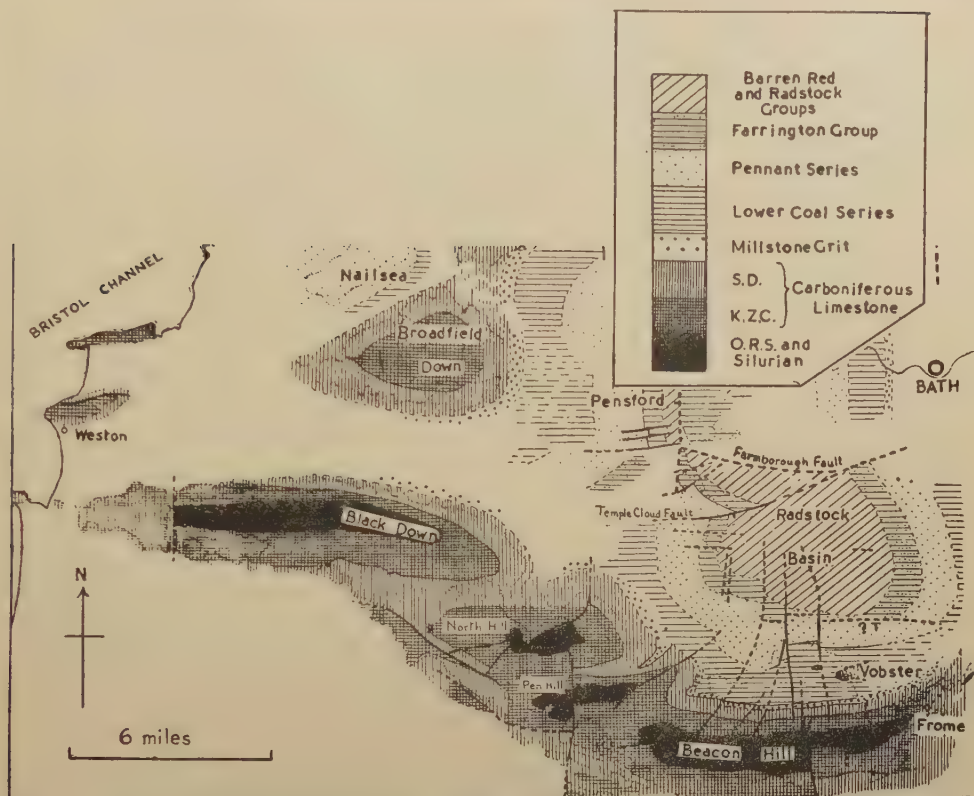


FIG. 2.—Diagram map of the four Mendip periclinal structures showing the structure of the Palaeozoic rocks.
(After Moore and Trueman, 1939, by permission.)

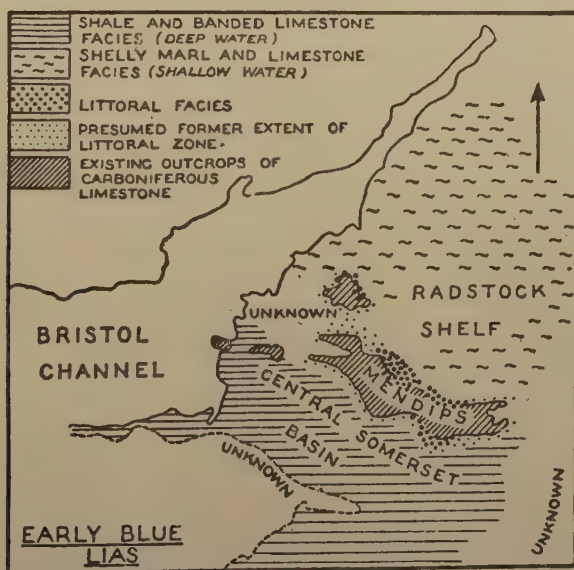


FIG. 3.—The distribution of the facies of early Blue Lias in Somerset.
(From Kellaway and Welch, 1948, by permission of H.M. Stationery Office.)

stable than the depression south of the Mendip periclinal. The relative stability of the Coalfield area compared with the southern depression was demonstrated again in Lower Liassic times (see fig. 3). The physiography of the Mendip area in Permian and Triassic times was therefore that of a ridge of high relief, controlled by the four periclinal, separating two areas of low ground to the north and south.

During Permian and Triassic times the high ground was eroded. The debris was deposited to the north and south by intermittent torrents, as pebbly sands and silt, and windblown dust was waterlaid in temporary shallow pools. Deposits of gypsum, celestine and rock salt indicate the presence of saline lakes in these areas towards the end of the Trias. Within the Triassic Mendip Hills scree of angular rock debris, or more rounded pebbly torrent deposit, began to fill up the valleys and accumulated on the hill slopes. The scree-torrent deposits are known as the Dolomitic Conglomerate, and they, and the sands and marls, are often bright red, due to the presence of finely disseminated haematite. The haematite may have been derived from the pyrites present in Coal Measure shales, by weathering and oxidation. The youngest Triassic deposits are often pale green, indicating a change in conditions of deposition.

By the end of Triassic times, relief in the Mendip periclinal had greatly diminished. In the two eastern periclinal over 11,000 feet of Carboniferous rocks must have been removed from the central parts of the folds, and in three of the four periclinal a central core of Upper Old Red Sandstone rocks was exposed. The most easterly periclinal, Beacon Hill, may have had the Old Red Sandstone core breached and Upper Silurian rocks exposed. The late Triassic relief achieved in the most westerly periclinal, Blackdown, contrasts with that of the other three. Part of it displays inverted structural relief. The western part of its Old Red Sandstone core was eroded to form a valley whose walls, formed of Carboniferous Limestone, were the northern and southern limbs of the periclinal. The central valley contains a filling of Dolomitic Conglomerate and Red Marls, and the northern and southern limestone walls were breached by other Triassic valleys. The other three periclinal had central cores of Upper Old Red Sandstone or Silurian rocks which formed the highest ground, and the structural relief thus remained uninverted.

At the close of the Triassic the Rhaetic Sea invaded Great Britain. Parts of the Mendip periclinal were not immediately submerged, some of the former high ground remaining above sea level as islands, and the Rhaetic deposits become thinner and more littoral in character as they approach these islands. The succeeding marine deposits, Liassic, and Lower and Middle Inferior Oolite, show that the islands were subject to encroachment by the sea, with intermittent periods of recession and erosion of previously formed littoral sediments. It is probable that the islands were completely submerged in Upper Inferior Oolite times, although positive evidence is available only at the eastern end of the Mendips, where outcrops of Upper Inferior Oolite have been preserved together with their relation to the underlying rocks.

The present condition of the Mendip Hills is due to the fact that post-Mesozoic erosion has stripped off much of the softer covering of younger Mesozoic rocks, while the more resistant Palaeozoic and Dolomitic Conglomerate rocks have been less affected. This process of exhumation has revealed much of the older, Triassic, topography. Today, as in Triassic times, the Mendips form a ridge of hilly ground separating more low-lying areas to the north and south.

THE FISSURES OF THE MENDIP AREA.

At least four different types of fissure occur in the area. Two of them originated under the sea and are filled with marine deposits which may be Rhaetic to Inferior Oolite in age. The other two are terrestrial phenomena and are Triassic in age. The marine types will be discussed first.

The Neptunian Dyke. The characters of certain fissures suggest that they originated under the sea as open clefts or cracks in the older rock forming the sea-floor. In the Mendip region the cleft was usually an opened joint or bedding plane in the

Carboniferous Limestone, which probably gaped as the result of small tensional forces operating on the limestone in the area. The cleft was long in proportion to its width, had sub-parallel walls, and a fairly straight course. The long cleft was filled with the debris which shifted about on the floor of the Rhaetic or Jurassic sea. This was the type of fissure known to Charles Moore.

Two neptunian dykes were described by Kühne. One was exposed during quarrying operations at the *Microlestes* Quarry at Holwell, and yielded all but one of the mammalian teeth found by him (Kühne, 1946). The other, still exposed at Windsor Hill Quarry, Downside, near Shepton Mallet, yielded abundant dissociated bones of *Oligokyphus*. Other dykes of this type occur in the eastern part of the Mendips, near to the outcrops of Rhaetic and Jurassic rocks. Care must be taken in estimating their age. The fillings may contain a mixture of pebbles with fossils ranging from Rhaetic to Inferior Oolite in age, but only the youngest elements indicate the time when infilling occurred. The dykes were situated close to the Jurassic Mendip islands, and the derived material suggests that the marginal Jurassic seas left thin deposits which were periodically reworked. The derived material found in these dykes is of interest, as it provides evidence bearing on the original extent of former thin sedimentary covers which were removed during short periods of Jurassic erosion.

As a possible source of Rhaetic or Jurassic terrestrial vertebrates the neptunian dyke offers two possibilities. One is exemplified by the Holwell dykes, the other by the dyke at Windsor Hill. In the Holwell dykes the mammalian teeth were almost certainly derived fossils of Rhaetic age redeposited in the fissure in Inferior Oolite times. The labour involved in securing them was considerable. The material sorted by hand by Charles Moore included about 70,000 fish teeth and yielded 29 mammalian teeth. Kühne washed about 2,250 kg. of clay from his 'Holwell 2' fissure and handpicked a concentrate of about 121 kg., which yielded 19 mammalian teeth.

The Windsor Hill neptunian dyke presents a different yield of terrestrial vertebrate bones. In this case the bones are abundant over a limited part of the fissure, and sparingly distributed over a rather greater part of its length. They are all dissociated, but are evidently not derived, as they are hardly waterworn and not limited to the most durable elements such as teeth. Kühne suggested that during Liassic (Charmouthian) times the fissure opened under the sea, close to the shore of one of the Jurassic Mendip islands. Occasional heavy rains swept the bones of *Oligokyphus* from the land surface into a brook, and so out to sea. The fissure, being close to its mouth, trapped the heavier particles of the stream's load, including the bones. Thus rainwash and the stream were one factor in the areal concentration of the bones, and the fissure was a further factor. The state of preservation of the bones suggests that the journey to their place of deposition was short and that burial was rapid.

Neptunian 'sagged-cover' dykes. This type of fissure also originated as a gaping joint or bedding plane of the Palaeozoic rock which formed the Rhaetic or Jurassic sea-floor. But when the crack gaped a thin sedimentary cover already existed above it, and this cover was let down into it. The cover deposits partially lined the sides of the crack, but were also partially disrupted to form clots and fragments filling the centre. Angular fragments of the walls were often included in the fissure filling. The rest of the filling consisted of contemporary marine deposits, sometimes almost horizontally bedded, which constitute the matrix of the coarser fragmental material.

An example of this type of fissure occurs just over a mile north of Gurney Slade. There are three exposures of the same fissure, which runs in an east-west direction. In a field on the west side of the road from Gurney Slade to Old Down is an old quarry. A vertical wall of rock has been left unquarried, as inferior stone, and stands isolated on the grass-grown quarry floor. This is the western part of the fissure. A steep-sided outcrop of Carboniferous Limestone, about 15 feet high, follows the east side

of the road, and the fissure is exposed here in cross-section. East of the road, and behind this outcrop, is a disused quarry named Cockhill, in which the eastern part of the fissure is exposed (Pl. 4, and fig. 4).

This fissure filling consists of Triassic and Liassic sediments. The Trias is usually fine-grained and may be well-laminated: a coarse conglomeratic facies is developed higher up on the south side of the western exposure of the fissure. The Trias is usually red, but occasionally a buff colour occurs. The Lias is most commonly a grey, comminuted shell limestone, with small conglomerate pebbles rarely larger than a quarter of an inch in diameter. Variations from this lithology occur, and a fine-grained limestone crowded with well-preserved fossils, or a coarse conglomerate, is sometimes developed. The conglomerate pebbles are usually quite well-rounded and include quartz, chert, Carboniferous Limestone and occasionally Trias. The Liassic fauna consists of lamellibranchs, gastropods, a rhynchonellid and an echinoid. The fauna was submitted to Dr. L. R. Cox and Dr. H. Muir-Wood. Their identifications, tabulated in an appendix, suggest that the deposit is Lower Liassic, probably Upper Hettangian. No evidence has been found to indicate that the Liassic sediments vary in age in different parts of this fissure.

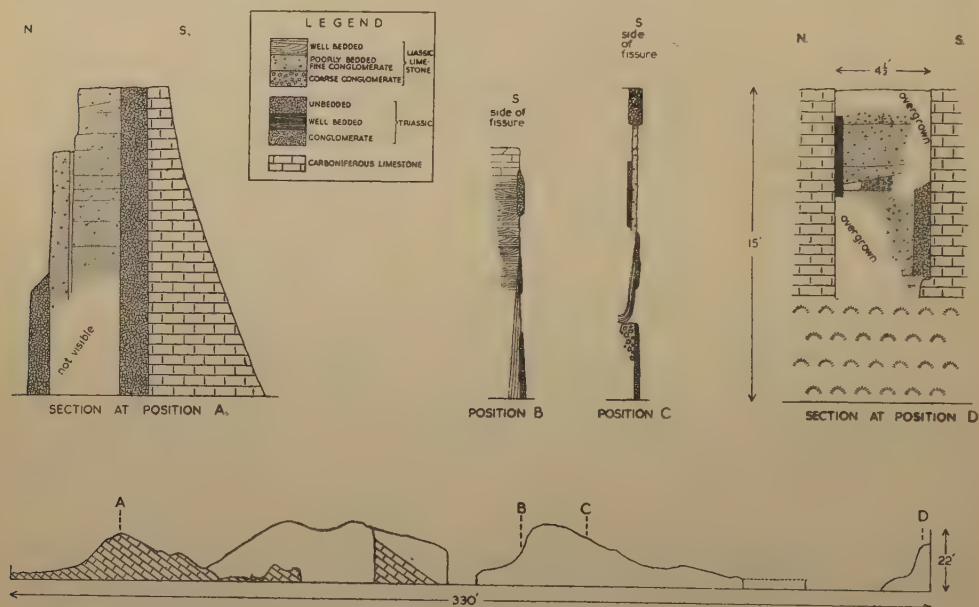


FIG. 4.—The western part of the Gurney Slade fissure. Lower diagram: The western part of the fissure seen from the south; Mesozoic rocks left blank.

The way in which the fissure and its filling originated is suggested by the character of the walls, and the disposition of the Triassic and Liassic sediments. The Carboniferous Limestone walls of the fissure are not waterworn. They are usually vertical and plane, but in places form irregular projections. It seems unlikely that the fissure was formed by solution of the limestone, but rather that it originated as a cleft which gaped as the result of small tensional forces acting in the locality. The Triassic fissure deposits occur chiefly as two vertical sheets, one lining each wall of the fissure (fig. 4). Where a lamination is developed this is directed vertically. The sheets of Trias are broken in places, and the broken edge may curl towards the interior of the fissure filling so that the edge is embedded in Liassic sediment. Detached fragments of the Triassic lining material lie in the more interior deposits

of the fissure. Within the outer lining of Triassic material there may be a second, inner, lining of Liassic sediments. In places these Liassic sediments are finely bedded, and the bedding dips vertically until it approaches the lower part of the fissure, when the dip becomes almost horizontal and is directed towards the interior of the fissure filling. Where the Triassic lining is absent, due to breakage, the Liassic lining lies adjacent to the wall of the fissure. The more interior fissure filling consists of Liassic material. This may exhibit an almost horizontal bedding, which usually displays a sharp discontinuity with that of the sedimentary linings of the fissure walls. Frequently the more interior Liassic fissure deposits show a rather confused arrangement which suggests that clots of Liassic material are embedded in rather similar sediments. The distribution and arrangement of the Triassic and Liassic sediments suggests that, prior to the opening of the fissure, a very thin deposit of continental Trias, with small pockets of conglomerate, covered the Carboniferous Limestone in this locality. In Upper Hettangian times a thin veneer of marine deposits was added above the Triassic cover. The fissure then opened and the two sedimentary covers sagged into it, partly lining the fissure walls and suffering a partial disruption in the process. After the fissure opened the deposition of Upper Hettangian sediments continued, formed a matrix to the fragmental material, and accumulated until the fissure was filled.

No vertebrate fossils were found in the Gurney Slade-Cockhill fissure. The possibility that such fissures will yield terrestrial vertebrates is probably rather less than in the case of the neptunian dyke. They were probably less efficient as traps, because when formed they were immediately partly filled by the cover deposits. If the cover deposits had included a bed containing terrestrial vertebrate remains then these would be preserved in the fissure even if subsequent erosion had removed them from their undisturbed position on the Palaeozoic rocks in the vicinity. As in the case of the neptunian dyke, the possibility of finding terrestrial vertebrate remains in this type of fissure depends to a considerable extent on the position of the fissure in relation to the Jurassic Mendip islands, and to the agents of transport obtaining at the time.

Subaerial fissure. This type of fissure is Triassic in age and terrestrial in origin. Its character suggests that it originated as a crack in the Carboniferous Limestone, which opened on the Triassic land surface, and became filled with surface rubble. An example can be seen at Torhill Quarry, about half a mile east of Wells, on the Wells-Shepton-Mallet road. The fissure has subparallel walls which show no sign of water-wear. The Triassic filling is a breccia, composed of sharply angular fragments of Carboniferous Limestone, with a red matrix of more finely grained sediments. The filling shows no trace of bedding and is completely unsorted. No fossils were found in it.

Underground watercourses. At the present day underground watercourses are in process of formation in areas where hard, well-jointed and bedded limestones are being subjected to the action of rainwater containing traces of carbonic acid. The rainwater quickly finds its way down the joints and bedding planes, and gradual solution of the limestone walls along its route produces a system of underground watercourses.

As soon as erosion had stripped the Coal Measure rocks from the Triassic Mendip Hills the underlying Carboniferous Limestone was exposed to the action of rainwater. Underground watercourses formed, and eventually filled with Triassic sediments; they are occasionally exposed in quarrying the Carboniferous Limestone. This type of fissure can be recognized by the following characters.

The fissure filling is usually enclosed by a limestone roof, as well as limestone walls and floor (fig. 5). The limestone boundary walls are usually irregular in cross section, in plan, and in profile. In places they swell to form small caverns (Pl. 1), in other places they form narrow irregular passages or mere cracks in the limestone. The walls are usually waterworn, and are often coated with stalactite. The sediments of the fissure-filling are often well bedded (Pl. 1), sometimes displaying small

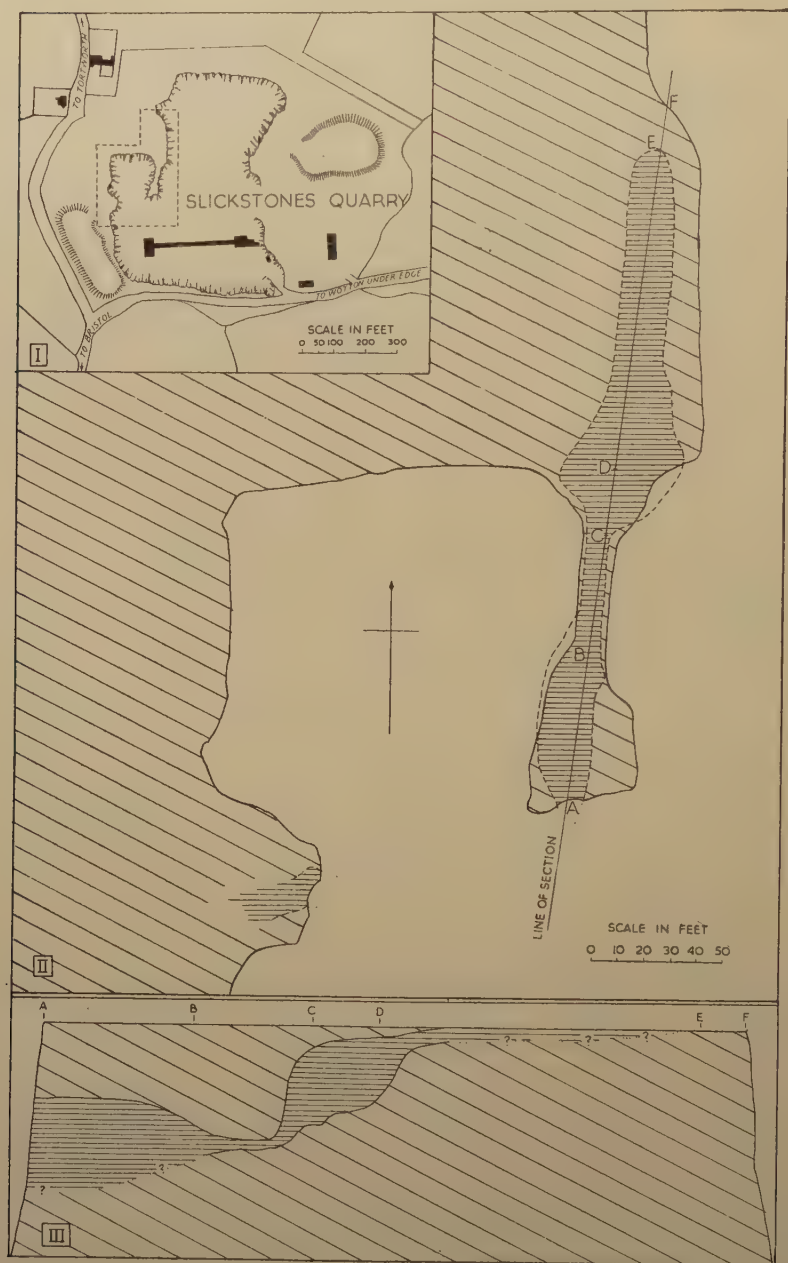


FIG. 5.—The Slickstones Quarry fissure.

scale current bedding. The bedding is usually nearly horizontal, although sometimes compaction of the sediments may have resulted in a considerable sag-curvature of the bedding planes. The sediments are sometimes conglomeratic, the fragments being Carboniferous Limestone. Pieces of stalactite, and recrystallized cave pearls,

are sometimes present in these fissure fillings. The best examples of this type of fissure are exposed at Batcombe Quarry, near Cheddar, in the Mendip area; and at Slickstones Quarry, near Cromhall, in Gloucestershire (see fig. 5 and Pl. 1).

The only invertebrate fossils which have been found in these Triassic watercourses are occasional specimens of *Euestheria minuta* (Alberti in Zieten) and derived Carboniferous Limestone forms. Not all of the Triassic underground watercourses, which appear in the course of quarrying operations, contain terrestrial vertebrates. But a high proportion of them contain at least a few bones. These may be a few poor fragments, sparsely distributed through a part of the fissure filling. But often a real bone bed is present in a certain part, or parts, of the watercourse, always near to the end at which water entered. The Triassic terrestrial vertebrates listed in Table 1 have all come from underground watercourse deposits.

THE AGE OF THE 'TRIASSIC' FISSURE DEPOSITS.

The age of the underground watercourse sediments, and the bones which they contain, is not easy to assess. They are of continental origin and could therefore have been deposited at any time during the Permo-Trias, indeed in a few limited areas they could be Rhaetic or Jurassic. Their sedimentary fillings form isolated pockets, and it has not been possible to trace a connection between them and the main Permo-Triassic outcrop. Even if this could be done it would not help matters, for, except at one or two localities, the Permo-Trias of the area is barren of fossils. The vertebrates found in the watercourse deposits are new genera; they belong to sauropsid groups whose early Mesozoic history is often only sketchily known, and there are few places in the world where a good sequence of fossiliferous horizons of Permo-Triassic continental rocks have been found.

In the Bristol Channel area the earliest dated horizon of Mesozoic age is the base of the Rhaetic. As conventional methods cannot be used, other means have had to be employed in dating the continental underground watercourse sediments. Three lines of approach to the problem have been found. A consideration of the probable history of the formation and infilling of the Triassic underground watercourses allows one line of evidence to be suggested regarding a probable age for their deposits. This is applicable in a general way to all the watercourses in the Bristol Channel area. A second line of evidence is supplied by the Emborough Quarry watercourse, and is based on a detailed study of this locality. A third line of evidence is based on the general character of the vertebrate fossils found in the fissure deposits.

The history of the underground watercourses may now be considered and the Mendip area used as an illustration. The formation and infilling of the underground watercourses is regarded as controlled by the relief and position of the water-table, and the history of the water-table in respect of these two factors is closely connected with the erosional and depositional history of the district in Permo-Triassic times.

At the sites of the cores of the Mendip periclinal ridges over 8,000 feet of Coal Measures and nearly 3,000 feet of Carboniferous Limestone were removed by erosion during Permo-Triassic times. It is not necessary to postulate that the Permo-Triassic Mendip Hills ever had the great relief which these figures suggest, as uplift and posthumous movement of the periclinal ridges during the two periods may have rejuvenated relief and kept active erosion in progress. Indeed the presence of narrow valley heads, filled with Dolomitic Conglomerate, which may extend up into the Old Red Sandstone core of some of the periclinal ridges, suggests that even at a late stage of general denudation of the whole ridge youthful valley-forms existed, and mechanical erosion was active until very late in Permo-Triassic times. The underground water channels, formed after the Carboniferous Limestone had been exposed by denudation, imply the existence of a certain amount of rainfall, and thus the presence of a water-table in the area.

While Permo-Triassic topographic relief was still well defined and before rock-waste had banked up the slopes and filled the valleys and neighbouring lowlands, the water-table must have had a fair relief over the whole area, and in the hills its level

probably fluctuated considerably. Such conditions, promoting the flow of subsurface waters, would be most favourable to the formation of underground water channels in the hilly region. In the higher ground the level of the water-table must have fallen, relative to rock horizon, as denudation and uplift proceeded. General lowering of the surface, which continued until late in the Triassic, must have removed much of the earlier formed watercourses, and only the deeper parts of these, or those formed late in the Triassic, can have been preserved. Little sedimentation can have taken place in the underground water channels until the water-table reached a minimum level towards the end of the Triassic. Thus the period of formation of the water channels, when solution of limestone was the dominant process, rather than deposition of sediments, continued from the time when the Carboniferous Limestone was exposed until late in Triassic times.

Towards the end of the Triassic, as relief was planed down in the hilly area and the neighbouring lowlands filled with sediments, the water-table must have become more uniform in level over the whole district, and therefore relatively stagnant. Within the hilly area, towards the close of the Triassic period, the filling of the valleys may have produced a slight general rise of the water-table, owing to the disappearance of the small-scale relief features and the continued banking up of the lowlands. These two factors, the greater stagnation of the water-table over the whole district and the slight rise of the water-table within the hilly area, led to the silting up of the underground watercourses, for run-off waters entering solution channels filled with water would soon have their velocity checked and deposit their load. It is not suggested that the silting up of the underground watercourses occurred synchronously over the whole of the Bristol Channel area or even in the Mendips—indeed a sequence of infilling would be expected. But the period in which deposition was the dominant process in the underground water channels was of short duration relative to the length of Permo-Triassic time, and it occurred late, just prior to the Rhaetic invasion. As the sea did not cover the entire Mendip area until Middle Jurassic times, nor quite submerge the Carboniferous Limestone outcrops of Glamorgan until Lower Liassic times, there remains the possibility that some of the watercourses continued to fill with terrestrial sediments after the Rhaetic invasion. In all the fossiliferous underground watercourses discussed in this paper, and listed as Triassic in Table I, except that at Higheroft Quarry, marine Rhaetic can be shown to have covered the site of the fissure. The underground watercourse deposits of the Bristol Channel area and the terrestrial vertebrates which they contain, are therefore probably Upper Triassic in age.

A study of the Emborough locality provides evidence regarding the age of its watercourse sediments. Emborough Quarries are situated on each side of the railway line running from Radstock to Shepton Mallet (see fig. 1 and Pl. 4). The entrance to the Quarries is on the Radstock-Wells road between Emborough and Old Down, about six miles north-east of Wells. The Triassic deposit in which the reptilian bones were found is situated in the eastern quarry. The limestone face has been worked back on each side of the Triassic deposit, so that the latter, left rejected as inferior stone, forms a projection which juts out from the eastern face. The end of this Triassic projection faces approximately north-west, and the two sides face approximately north-east and south-west (Pl. 4).

The south-west side consists mainly of Carboniferous Limestone which has the same dip and strike as that of the adjacent quarry face. It represents one of the lateral walls of the watercourse. In its lower part some of the joints and bedding planes are waterworn, with small swirl-holes filled with finely bedded red clay. The Carboniferous Limestone on this south-west side forms a very thin flanking wall left in contact with the watercourse deposits, and most of the projection consists of a mass of Triassic sediments (Pl. 3).

The Triassic sediments can best be seen on the north-west end of the projection (Pl. 2). The lower part of the mass consists of a homogeneous, well-bedded, micaceous clay, dark red in colour but with occasional streaks of green. The upper

part is a conglomerate in which large boulders of Carboniferous Limestone, up to several tons in weight, are set in a matrix of limestone pebbles, flakes of a pale shale, and silt. In places, where the silt is pebble-free, it is finely bedded. The silt is usually deep red, but occasionally a pale green colour is developed, either as patches or as alternate laminae in the bedded silt. Pieces of stalactite have been found in this conglomerate. The large boulders are usually waterworn on one or two of their faces, the others being angular fracture surfaces. Both the worn and the angular surfaces lie embedded in the mass of pebbles and silt, showing that the condition of the boulders was produced before the deposition of the surrounding sediments. There is an abrupt change in deposit from the lower homogeneous clay to the conglomerate above.

The north-east side of the Triassic projection has been much obscured by the tipping of quarry rubbish. The visible sediments are all of the conglomeratic type. The lateral wall of limestone which should lie in contact with the Triassic sediments on this side has been quarried away. The fossil bones occur towards the top of the upper, conglomeratic sediments, on the north-west and north-east side of the projection.

The whole Triassic deposit is interpreted as the sediments of a cave, forming part of an underground watercourse. At a certain stage in its history the cave roof and part of the sides collapsed. The homogeneous, well-laminated clay, which forms the lower part of the deposit, represents the fine sediments laid down in the cave before the collapse occurred. It suggests that the coarser and heavier part of the stream's load had been dropped before this cave was reached. At this stage, therefore, the cave may have been some distance from the intake end of the watercourse. The conglomerate, which begins abruptly above the clay, represents the collapsed roof and upper sides of the cave. When collapse occurred the cave would be in direct communication with the land surface, having become a depression filled with limestone blocks. The silting up of this depression would be partly due to the stream running through the bottom of it, but mainly due to the trapping of rainwash from the surrounding land surface. The fossil bones were found towards the top of the conglomerate: they are not found in the lower part, nor in the clay deposited prior to collapse. It is probable that they were swept into the depression, with other debris, from the surrounding land surface after periods of rain.

The presence of such a large number of limestone blocks in the conglomerate suggests a total collapse of the cave roof, as distinct from the dropping of a few unstable blocks. This indicates that just before the collapse occurred the cave roof had become quite thin, the contemporary land surface lying perhaps only a few feet above. If the age of this land surface could be estimated it would provide an approximate date for the collapse of the cave. The age of the debris and reptile bones filling the collapse depression would then be post-collapse and pre-Rhaetic.

In order to form an estimate of the age of this Triassic land surface it is necessary to study the Mesozoic topography developed on the Palaeozoic rocks of the area round Emborough Quarries. The Palaeozoic rocks of this area form the eastern part of the Pen Hill pericline (fig. 2). In the discussion which follows it should be borne in mind that the Mendip Hills were not a glaciated area in Pleistocene times, but were subjected to periglacial conditions. In the Emborough area the effects of the periglacial climate are not very striking and were possibly limited to the break-up of part of the thin Jurassic cover by frost-action, followed by incorporation of the resulting blocks into a subsoil rendered pasty by thaw.

The Mesozoic topography falls into two categories. A Triassic topography of hill and valley showing a fair degree of small scale relief has been buried and to some extent re-exposed. This topography can be shown by mapping the distribution of the Dolomitic Conglomerate. The map (Pl. 4) shows that the Conglomerate fills a small narrow valley to the south and south-west of the Quarries, and the outcrop then curves northwards and finally westwards. In its northward and westward course the Conglomerate outcrop is following round the curve of a hill of

Palaeozoic rocks and is banked against its slope. The spur of the hill coincides with the 'nose' of the Pen Hill pericline; the Triassic valley was eroded in the zones of the Carboniferous Limestone which form the Binegar syncline. Emborough Quarries, and the Triassic cave, lie on the spur.

The other element of Mesozoic topography is more closely related to the present surface and is shown on the map (Pl. 4). The land surface slopes gently from about 800 feet in the southern part of the map to about 700 feet in the northern, and passes across the Palaeozoic rocks and the Dolomitic Conglomerate. Quaternary and recent erosion has begun to dissect this surface by cutting down from it a series of narrow winding valleys. The land surface passes across the top of the Emborough Quarry faces and also across the Triassic cave-deposit. To the north of the Quarries, it is cut by a narrow valley, but can be seen again further north where the Quarry offices and plant are situated.

This surface, which slopes gently northwards, is that on which the Rhaetic and Jurassic sediments were laid down, for small isolated patches of these rocks still lie on it in places. At the entrance to Emborough Quarries, at the northern edge of the map, part of the main outcrop of the Rhaetic appears. Here it is only 15 feet thick, and consists mainly of black shales, pale clays, and grey sandstones which weather yellow (Morgan & Reynolds, 1899). This outcrop is now overgrown. Four hundred yards south of the Rhaetic outcrop, at the top of the face in the eastern quarry, where the land surface is present, occasional fragments of black shale and blocks of a yellow sandstone containing plant fragments and casts of small lamelli-branches can be found in the subsoil above the Carboniferous Limestone. There is little doubt that these are remanent fragments of a former Rhaetic cover, leached by subsoil weathering. The lithology of the sandstone is quite different from that of the later Jurassic rocks in this area. South of Emborough Quarries the neptunian sagged cover dyke, described in a preceding section, preserves a sample of a former Mesozoic cover which has since been stripped off at this locality. No Rhaetic could be detected in the dyke. It is possible that a Rhaetic cover existed here and was stripped off in pre-Liassic times, but this seems unlikely as the thin, often finely laminated, Triassic cover would also have been removed. The Rhaetic which occurs at the entrance to Emborough Quarries is thin, and it seems more probable that the Rhaetic feathered out between Emborough Quarries and the dyke. South-east of Gurney Slade occurs a silicified sandy rock marked on the old Survey Map (O.S. 1 inch, sheet 19), as Lias, but the contained fossils (see Appendix II) prove that this rock is actually Inferior Oolite.

If this land surface represents the plane of the Rhaetic-Jurassic transgressions, then it also represents, in an approximate way, the final surface of relief achieved here at the end of the Triassic, slightly trimmed by the invading seas. From its present position in relation to the Emborough cave deposit there is little doubt that it must lie only a few feet below the Triassic land surface which existed hereabouts at the time when the cave collapsed. The Triassic collapse-surface must therefore represent a very late stage in general denudation of the area; the last few feet of more than 8,000 feet of rock removed from this part of the pericline. The debris and bones which filled the collapse-depression in this surface must therefore have been deposited late in the Triassic period.

The character of the vertebrate fauna obtained from the Triassic fissures of the Bristol Channel area provides some evidence of its age. Von Huene (1940), who studied the Permian and Triassic faunas of the 'Gondwanaland' areas, the United States, Scotland, and Russia, has shown that during the Middle Triassic a marked faunal change occurred. In the earlier part of the Triassic the mammal-like reptiles are the commonest faunal elements: diapsids are relatively rare. In the Upper Triassic the diapsids are the common forms, the archosaurs in particular having begun a radiation into a number of orders and families, and the mammal-like reptiles have become extremely rare and 'advanced' in structure. No mammal-like reptiles have been found in the Triassic watercourse deposits to date. The fauna consists entirely of diapsids and protorosaurs.

Thus the Triassic fissure faunas are, in general character, Upper Triassic in type. The geological evidence suggests that they are late Upper Triassic in age, both on the general hypothesis discussed above, and on a different line of evidence obtained from the study of a single locality. This suggests that the faunas from each locality may possibly form part of a larger Bristol Channel fauna of late Triassic age. The distribution of the members of the Bristol Channel fauna adds a little weight to this last suggestion, although the areal distribution of reptiles is still inadequately known. The reptile commonest in the Emborough fissure deposit also occurs at Batscombe Quarry, Cheddar, and is present as a rarity in the 1951 Slickstones material. This Slickstones deposit also contains a small reptile, probably a lepidosaurian, which has a very characteristic dentary. Several specimens of an exactly similar dentary have been found in the Pant-y-flynnon fauna, from near Cowbridge. The fact that two reptiles occur at more than one locality is suggestive. If this were the case with one form only it might be an ubiquitous species with a fairly long range in time. It is hoped that further preparation of material will reveal other forms which allow cross-correlation between localities.

The available evidence for age, whether supplied by the vertebrate fauna or from geological investigation, is corroborative. It suggests that the watercourse deposits discovered to date are late Triassic, and the terrestrial vertebrates which they contain form a Bristol Channel fauna of this age. It is hoped that the geological evidence of the age of the Bristol Channel fauna, relative to the Rhaetic invasion of western Britain, may be helpful in assessing correlation between the horizon of its fauna and horizons of continental vertebrates in other areas.

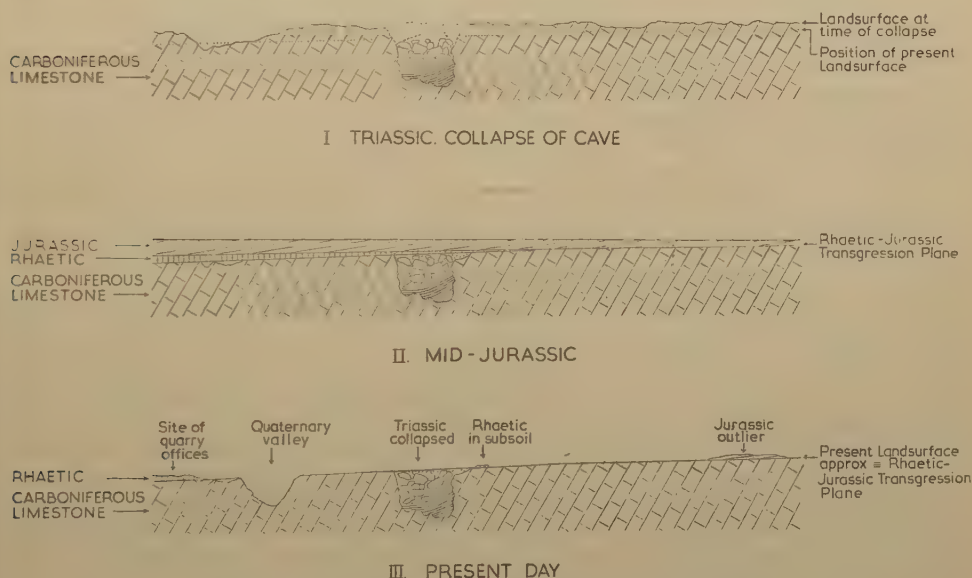


FIG. 6.—The history of the Emborough Quarry fissure.

LATE TRIASSIC CLIMATE AND VEGETATION IN THE BRISTOL CHANNEL AREA.

A characteristic feature of the Triassic rocks in the area is the prevailing red colour. This red colour is usually absent towards the top of the Trias, and may be absent locally at any part of the period. Although the mode of formation of such red beds is a subject of controversy no one has yet suggested that extensive deposits of them were formed under temperate, cold wet, or cold arid conditions. The climatic conditions which have been suggested as necessary for their formation are either hot and dry, or hot and humid.

Under hot humid conditions chemical weathering plays the more active role in rock destruction, and under its influence only the most stable minerals are preserved. Fragments of Old Red Sandstone, obtained from the Dolomitic Conglomerate, show no signs of the effects of chemical weathering and still retain occasional chips of fresh microcline feldspar. An analysis was made of the sediments in the Emborough Quarry fissure. 92 per cent of the light mineral fraction consisted of flakes of feldspar. The feldspar may be partly derived from the Old Red Sandstone, but the non-calcareous residue of one of the types of limestone present in the eastern quarry at Emborough consisted mainly of cleavage flakes of feldspar. The survival of such a quantity of feldspar flakes in the cave sediments (in both pre- and post-collapse deposits) suggests either that hot and humid conditions prevailed but that erosion and deposition was so rapid that the feldspar flakes had no chance of decaying before burial, or that deposition was at a moderate rate under semi-arid or arid conditions with chemical weathering at a minimum. Evidence which suggests that deposition in the underground watercourses was not at all rapid will be cited below.

Under arid or semi-arid conditions mechanical weathering is the more active agent of rock destruction and chemical weathering is slight. The spreads of Dolomitic Conglomerate, containing enormous numbers of fragments of Old Red Sandstone and Carboniferous Limestone, suggest that mechanical shattering, under arid or semi-arid conditions, was a very active process in Triassic times.

Evaporite deposits occur in the Upper Triassic of the lowland areas, to the S. of the Mendip range, to the N. of the Mendips and in S. Gloucestershire, and to a lesser degree in S. Wales. Their presence suggests a hot climate in Upper Triassic times, with a high rate of evaporation of saline lakes. Evaporites also suggest a low rainfall, for abundant rain would provide a copious supply of fresh waters entering the lakes and so check the effects of evaporation by continual dilution.

The presence of the underground watercourses, channels dissolved in the Carboniferous Limestone and filled with water-laid sediments, requires that a certain amount of rainfall should have occurred in Triassic times, at least in the hilly areas where the watercourses were situated. In view of the evidence for a semi-arid or arid climate, just reviewed, it is reasonable to postulate an intermittent rainfall which may have been moderately heavy but which occurred at infrequent intervals. The sediments in the underground watercourses provide some evidence in support of this suggestion. Most commonly they are well-laminated deposits (see Pl. 1), and mud cracks frequently occur in them, indicating that the watercourses often dried up. The mud cracks, which may be up to an inch across, are sometimes filled with small chips of limestone, fragments of calcite and crinoid ossicles, and similar material forms a thin layer through the channel deposit in continuity with the top of the mud crack. These mud crack fillings, markedly coarser than the average deposits of the channels, suggest the sudden onset of heavy rain which first brought in a load of coarser debris from the land surface above before contributing fine silt and clay.

The presence of *Euestheria minuta* in the underground watercourses of Pant-y-flyn and Slickstones Quarry, and its mode of occurrence in the main Upper Triassic outcrop, is also suggestive of semi-arid conditions with an intermittent rainfall. Present-day species of *Estheria* occur in temporary pools in slight depressions or 'vleys' in the sandy plains of S. Africa. Intermittent rains carry mud, dissolved salts, and fragments of the sparse desert flora into the pools; *Estheria* appears, flourishes, and then becomes buried in the mud as the pools dry out. The Upper Triassic *Euestheria minuta*, often occur in small lenticles of silt, sometimes containing salt pseudomorphs, suggestive of conditions similar to those seen today in S. Africa (see Neaverson, 1955).

Some vegetation must have existed in the Bristol Channel area in late Triassic times to support the fauna of reptiles which lived there. No trace of it has so far been found in the form of macrofossils, though the watercourse deposits still have to be examined for the possible presence of spores. A small flora was discovered at Bromsgrove in the Midlands, but it is earlier in age than the underground watercourse sediments (probably Upper Bunter, see Wills, 1948, p. 85). It is unlikely that the

vegetation which existed in the Bristol Channel area formed a close cover, as this would have retarded the mechanical weathering, whose importance has already been mentioned. A rather sparse vegetation best accords with the climatic conditions outlined above.

THE ACCUMULATION OF THE BONES IN THE UPPER TRIASSIC UNDERGROUND WATERCOURSES.

The fossil bones found in many Tertiary and Quaternary caves occur either in a cave-earth or in a drip-tufa deposit, usually in a cave near to the outlet end of the underground watercourse system. In such cases most of the bones were brought into the cave by animal locomotion, representing the remains of large and small animals which used the cave for shelter and also those of the prey of the carnivores.

The bones accumulated in the Triassic underground watercourses in quite a different way. They occur in water-laid deposits, always near to the inlet end of the watercourse system, and were brought in by stream-water from the surrounding land surface. Commonly the bones are well-preserved, and must have been buried quickly under a layer of silt. But sometimes the bones have been knocked about, broken, and even rounded up into bone-pebbles before being buried. Occasionally associated remains occur, skeletons or parts of skeletons. At the present day, in hot and fairly dry climates, the corpses of small terrestrial vertebrates may dry up quickly after death, becoming very light 'mummies' of bones and dry skin and flesh. If this also occurred under the semi-arid conditions of Upper Triassic times the light mummies of small dead reptiles could, in some cases, be washed down into the underground watercourses at the onset of a heavy rainstorm.* Once buried below ground under a layer of wet silt the skin and flesh would rot, but the skeleton might remain intact unless disturbed by the next wash-through of rain-water. Locally dissociated reptile bones are sufficiently numerous to form a bone-bed. This concentration of animal remains may be explained if the conditions on the land surface in Upper Triassic times are borne in mind. In the absence of a close vegetation cover a rainstorm might sweep the debris from a fairly wide area of land surface into the relatively restricted area of the nearest underground stream-channel, so effecting the concentration of animal remains.

THE UPPER TRIASSIC VERTEBRATE FAUNA.

One of the important features of the Upper Triassic Bristol Channel fauna is that its members lived on the higher ground of the continent of that period; a feature which emerges when the localities at which they have been found are plotted on a reconstruction of the relief in the area in Upper Triassic times. On high ground erosion is the dominant process, and therefore little is known of the faunas which have lived in such areas in the past, at least prior to Tertiary times. Most terrestrial vertebrate faunas of any period are lowland or coastal forms, for these are the main areas where deposition of sediment occurs. W. D. Matthew, when discussing dinosaur evolution in his book 'Climate and Evolution' (1939) wrote (p. 12): "The dominant order of land reptiles up to the close of the Mesozoic was the dinosaurs, pre-eminently a dry-land adaptation in their inception, since their most marked characteristic lies in their long limbs, bipedal progression and general parallelism in proportions and structure to the large ground-birds of modern times, which are today peculiarly the inhabitants of arid regions. The relationship and origin of the more specialized, mostly gigantic, dinosaurs of the later Mesozoic can best be explained by regarding them as a succession of derivatives from smaller and more lightly constructed upland dinosaurs, mostly unknown to us, the larger and more specialized types being re-adapted to a swamp life and inhabiting the coast marshes whose sediments are still preserved, while the more direct line of dinosaurian evolution inhabited the uplands, where the sediments, if such were deposited, have long since been removed by erosion, and the fauna is consequently unknown to us,

* A small reptile skeleton with part of the skin preserved has now (1955) been found in the Slickstones Quarry fissure deposit.

except by inference . . . if our knowledge of the Tertiary sediments were limited to the coastal swamp desposits, if in this country for instance we knew only the Tertiary of the Atlantic and Gulf coasts, we would be equally at a loss for any direct ancestral series illustrating the evolution of the mammalia". Matthew contrasts the record of the evolution of other terrestrial reptiles with the more adequate one of many of the swamp-dwelling, amphibious or littoral forms. The Upper Triassic reptiles found in the underground watercourse deposits of the Bristol Channel area, which lived on the denuded higher ground of that part of the North Atlantic continent, provide us with the only record known from Mesozoic rocks of a fauna of this character. When the members of this fauna have been described it will be interesting to compare them with faunas of the same period from the lowland areas of the North Atlantic continent.

Another feature of the whole fauna is the size of its members. The largest reptile present probably had an average size of about six feet. The smallest reptiles are as yet inadequately known, being completely dissociated, but their dentaries may be used as an indication of their size. Some of the small dentaries seem likely to belong to individuals representing growth stages of rather larger forms. Others, already known from a number of specimens, present a much narrower range in size and are all small. The smallest dentary is about 8 mm. long, and has a tooth row 4.5 mm. long bearing 12 teeth. Evidently some of the reptiles in this fauna were about the size of a modern wall lizard (*Lacerta muralis*). In the Triassic the diapsid reptiles began a radiation into the various orders which form the common elements of the Jurassic and Cretaceous faunas. An Upper Triassic fauna of small diapsids may be very valuable, as the small forms of any stock are held to be those with evolutionary potentialities, being free from the specializations which are the concomitant of large size.

In view of the age of this fauna and the size of its members the absence of mammal-like reptiles or mammals is particularly interesting. After the incursion of the Rhaetic-Liassic seas immediate evidence of such forms is sound. Possibly their ecological requirements were such that they moved northward, just in advance of the Rhaetic-Liassic sea which brought a change of climatic and other conditions to the areas on which it encroached.

British Triassic rocks are notoriously unfossiliferous. Occasionally a small fauna or flora is preserved. Such are the well-known Elgin reptile fauna, the small flora and fauna from the Bromsgrove area of the Midlands, and the Durdham Down reptiles from near Bristol. Elsewhere the usual record is a very occasional fragment. These scattered finds give the impression that the British part of the Triassic continent was not an area inimical to life, but rather that most of the life that existed was not preserved. The Upper Triassic watercourse fauna heightens the impression that an abundant and varied fauna existed on the continent of the period. The fossiliferous material from Emborough, Batscombe and Slickstones is so rich in bones that in some places it forms a bone bed. The preservation of the material is excellent, particularly at Emborough and Slickstones. That so little of the life of the Triassic period has been preserved in Britain is no doubt due to a number of factors. One of these factors may have been that the animal and plant remains were not buried quickly but were subject to the slow process of comminution at the surface. The underground watercourses probably afforded the only possibility of quick burial, and subsequent protection, of animal remains in their vicinity.

The underground watercourses of late Triassic times are thus of importance as a means of preservation of fossil bones and as providing a sample of a fauna from areas of relatively high ground at a time when the evolution of the sauropsid reptiles was at a particularly interesting stage, particularly in the case of the smaller representatives of the various groups.

ACKNOWLEDGMENTS.

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SUMMARY.

Terrestrial vertebrates have been discovered in Mesozoic deposits occurring as fissure fillings in the Carboniferous Limestone of some of the counties round the Bristol Channel (Somerset, South Gloucestershire, Glamorgan). These terrestrial vertebrates fall naturally into two groups: one group consists mainly of mammals and mammal-like reptiles, of Rhaetic or Lower Liassic age, which are found in fissures of submarine origin. Most of these fossils have already been described, and a summary is given of Kühne's studies of the fissures in which they are found. The other group consists of sauropsid reptiles only, found in a different type of fissure, of continental origin.

The paper is mainly concerned with the second group of reptiles and the fissures in which they are found. These fissures are shown to be small underground watercourses, formed during Permo-Triassic times when the area was part of a continent. The age of the sediments and reptile bones found in these underground watercourses is considered, and shown to be late Triassic, both on geological grounds and on the character of the fossil reptiles. The reptiles from different localities probably form part of a fauna, the Bristol Channel fauna, of late Triassic age.

In considering the age of the sauropsid reptiles a reconstruction of their physical background is outlined, and this is completed by a tentative sketch of climatic conditions. From this reconstruction emerges an important feature which characterizes the whole Bristol Channel fauna, namely, that the members of this fauna lived on the higher ground of the continent of the period. This is the only known example of a mesozoic fauna of this type, and when its members have been studied it will be interesting to compare them with those from the lowlands of the Upper Triassic continents.

The members of the Bristol Channel fauna identified so far are all diapsids and protorosaurs. During the Triassic the diapsids radiated into the orders and sub-orders whose members form the common elements of later Mesozoic terrestrial faunas. These late Triassic diapsids are therefore particularly interesting, especially as those of the Bristol Channel fauna are all small (less than six inches to over six feet in length) and therefore free from the specializations which are the concomitant of large size.

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APPENDIX I.

FOSSILS OBTAINED FROM THE GURNEY SLADE FISSURE.

BRACHIOPODA

Calcirhynchia calcaria S.S. Buckman Hettangian and basal Sinemurian.

LAMELLIBRANCHIA

Modiolus hillanoides Chapuis and Characteristic of the *angulatum* zone.

Dewalque

Myoconcha psilonoti Quenstedt *Planorbis* to *bucklandi* zones.

Chelamys textoria (Schlotheim) Long-ranging Liassic species.

Lima (*Plagiostoma*) sp. A relatively small form of the group *L. gigantea* (J. Sow.). Liassic.

Pseudolimea pectinoides (J. Sowerby) Long-ranging Liassic species.

GASTROPODA

Pleurotomaria cf. *cancellata* A species of the *angulatum* zone.

Terquem and Piette

Pleurotomaria sp.

Discohelix sp.

Eucyclomphalus sp.

Probably a new species.

Probably a new species. The genus is confined to the Lias.

Amberleya two sp.

One is probably a new sp.

Bourgetia ? sp.

Impression of base.

APPENDIX II.

FOSSILS OBTAINED FROM THE SILICIFIED ROCK MARKED AS LIAS ON THE OLD SERIES
ONE INCH GEOLOGICAL SURVEY MAP NO. 19.

(Identifications by R. V. Melville, Esq.)

Localities.

Specimens were collected from :

1. South-east of Badgers Cross, a mile south-east of Gurney Slade. The rock probably forms a disrupted cover in this area. When seen in an excavation blocks of the rock were embedded in the subsoil, and were very numerous. No blocks of limestone or Trias were present in the excavation, though the underlying solid rock in the area is Carboniferous Limestone. The exterior of the blocks was stained brown, presumably due to subsoil waters. Numerous blocks of the same rock occur in hedgerows, farm gateways, etc. in the area and all have the stained exterior except where they have been trimmed. No quarry of this stone exists in the Badgers Cross area so presumably all the blocks have been obtained from the subsoil in the locality. Specimens have been deposited at the Geological Survey.

2. Highcroft Quarry, about one-third of a mile south-west of Gurney Slade. Occasional blocks of rock are seen in the subsoil above the quarry face. Specimens have been deposited at the Geological Survey. The exterior of the blocks are stained brown. The blocks are sparser in their distribution in the Highcroft Quarry area than in the Badgers Cross area.

LAMELLIBRANCHIA

<i>Trigonia bella</i> Lycett	} Forms characteristic of the Inferior Oolite.
<i>Myophorella striata</i> (J. Sowerby)	
<i>Myophorella</i> (<i>Vaugonia</i>) <i>angulata</i> (J. de C. Sowerby)	
<i>Eopecten</i> cf. <i>velatus</i> (Goldfuss)	
<i>Plagiostoma</i> cf. <i>semicircularis</i> (Goldfuss)	
<i>Astarte</i> cf. <i>elegans</i> (J. Sowerby)	
<i>Gervillella</i> cf. <i>acuta</i> (J. Sowerby)	
<i>Lopha costata</i> (J. de C. Sowerby)	
<i>Camptonectes rigidus</i> (J. Sowerby)	
<i>Limatula gibbosa</i> (J. Sowerby)	

GASTROPODA

Trochotoma cf. *gradus* (Deslongchamps)

BRACHIOPODA

large sulcate Terebratulas

Liassic Terebratulas are non-sulcate.

ECHINODERMATA-CRINOIDEA

Isocrinus sp.

EXPLANATION OF THE PLATES.

PLATE 1 (a).

Photograph of the first cavern of the Slickstones Quarry underground watercourse, now cut across in transverse section near position D in text-figure 5 (II). Viewed from the south.

PLATE 1 (b).

Outline tracing of the photograph in Plate I a, to show the boundary between the Carboniferous Limestone and the Triassic sediments of the cavern.

1. Sediments of the cavern.
2. Part of the sediments of the narrow channel (see fig. 5) leading to the second cavern.
3. Carboniferous Limestone forming cavern walls and roof.
4. Carboniferous Limestone of the main (northern) face.
5. Carboniferous Limestone of the northern part of the eastern face (see fig. 5).

PLATE 2 (a).

Photograph of the N.W. face of the main Mesozoic deposit, Emborough Quarry.

PLATE 2 (b).

Traced Diagram, taken from the photograph of the N.W. face of the main Mesozoic deposit Emborough Quarry.

1. Limestone *in situ*.
2. Quarry rubbish.
3. Exposure of homogenous clay.
4. Conglomerate.

PLATE 3 (a).

Photograph of the S.W. face of the main Mesozoic deposit, Emborough Quarry.

PLATE 3 (b).

Traced diagram, taken from the photograph of the S.W. face of the main Mesozoic deposit, Emborough Quarry.

1. Pebbly stream deposit, completely surrounded by limestone.
2. Homogenous clay, about ten feet exposed.
3. Conglomerate of the N.W. face.
4. Limestone *in situ*.
5. Limestone of the main face.
6. Small water-worn swirl-holes in the limestone filled with well-laminated clay.
7. Water-worn bedding plane.

PLATE 4.

GEOLOGY OF THE AREA NEAR EMBOROUGH QUARRIES.

Palaeozoic boundaries after F. B. A. Welch (1929).

Mesozoic boundaries by the author. These differ from those on the Geological Survey 1-inch map, sheet 19 (Old Series), mainly as follows:—

1. The age of the outlier of Mesozoic rocks in the S.E. corner of the map has been shown to be Inferior Oolite, not Lias (see Appendix II).
2. An outlier of cherty Lias is indicated on the Survey map, occupying much of the ground between the Emborough Thrust and the Slab House Fault. On my map its boundary would run approximately from the G. in Emborough Thrust to the F in Fault, then along the fault as far as the 700' contour, there curving back to the Emborough Thrust so as to include the patch of Tea Green Marls.

Fragments of siliceous rocks were found in ploughed fields adjacent to the Thrust, and larger pieces in walls forming field boundaries there and as far east as the Slab House Fault. These rocks divide naturally into two groups. One consists of quartzite and sandstones, similar in lithology to those seen in the quarry in the Carboniferous grits W. of the ochre pockets. There seems no reason to suppose that these fragments are not Carboniferous, farmers having used material from the quarry for building or repairing walls. The second type of siliceous rock commonly has a dark blue compact 'heart', and a buff or cream-coloured 'skin' of varying thickness. Some large boulders of this type, obtained from the subsoil of one of the ochre pockets, contained Carboniferous Limestone fossils, which showed no sign of being derived fragments. Possibly the silicification, which has been shown to have affected rocks varying in age from Triassic to Inferior Oolite in this part of the Mendips, has affected the Carboniferous Limestone at this locality.

The only Mesozoic rocks which can be identified in this area are the ochre pockets and the two patches labelled Tea Green Marls. The age of the ochre pockets is uncertain, as no fossils could be found in them, but Morgan & Reynolds (1899) recorded ochre pockets within and below the Triassic conglomerates and sandstones formerly exposed near the Emborough Quarries offices. The patches labelled Tea Green Marls are bluish green clays which weather yellow, and form a very sticky clay soil. At the southern tip of the northern outcrop these clays may be seen resting directly on the Carboniferous Limestone. A similar clay, resting on red marls and followed by the basal Rhaetic bone bed, is recorded by Morgan & Reynolds from the pits formerly worked near the Emborough Quarries offices.

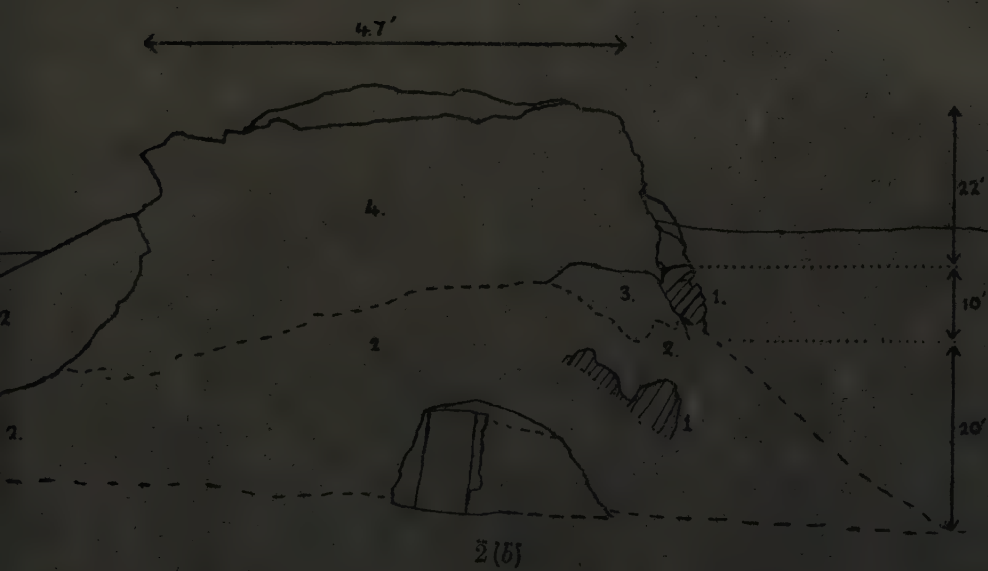






PLATE 1 (*a*).—The Slickstone Quarry fissure: the first cavern, at position D in fig. 5, now cut across by quarrying and viewed from the South.

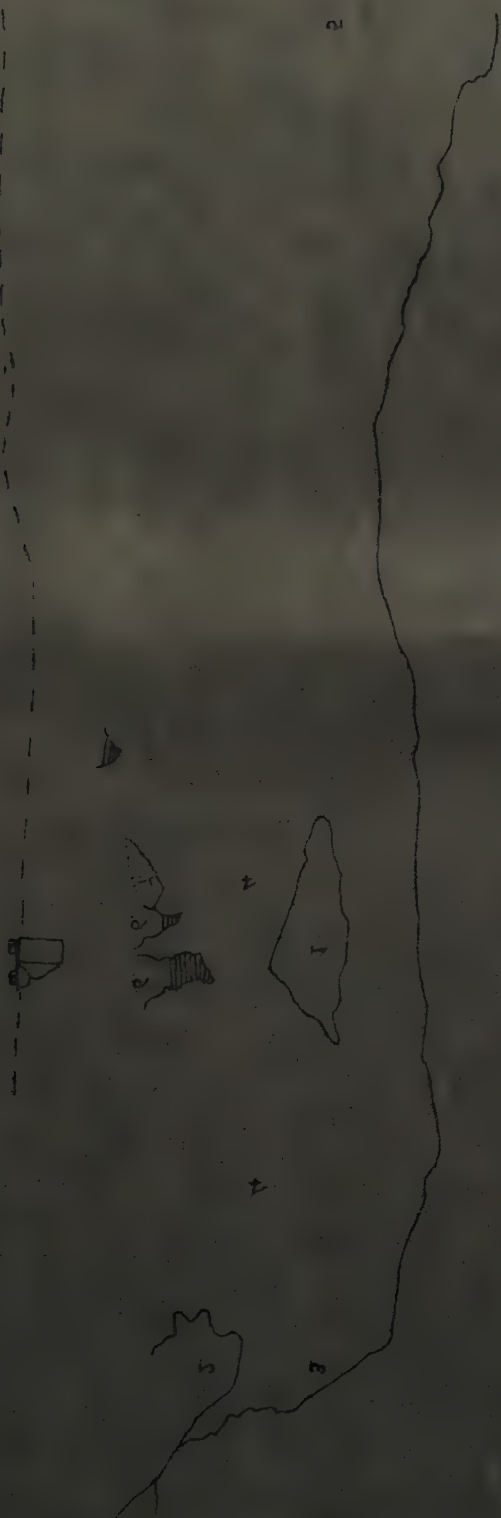


PLATE 2 (*a*).—The Emborough Quarry fissure: the north-west side.



PLATE 3 (a).—The Emborough Quarry fissure; the south-west side.

(5)





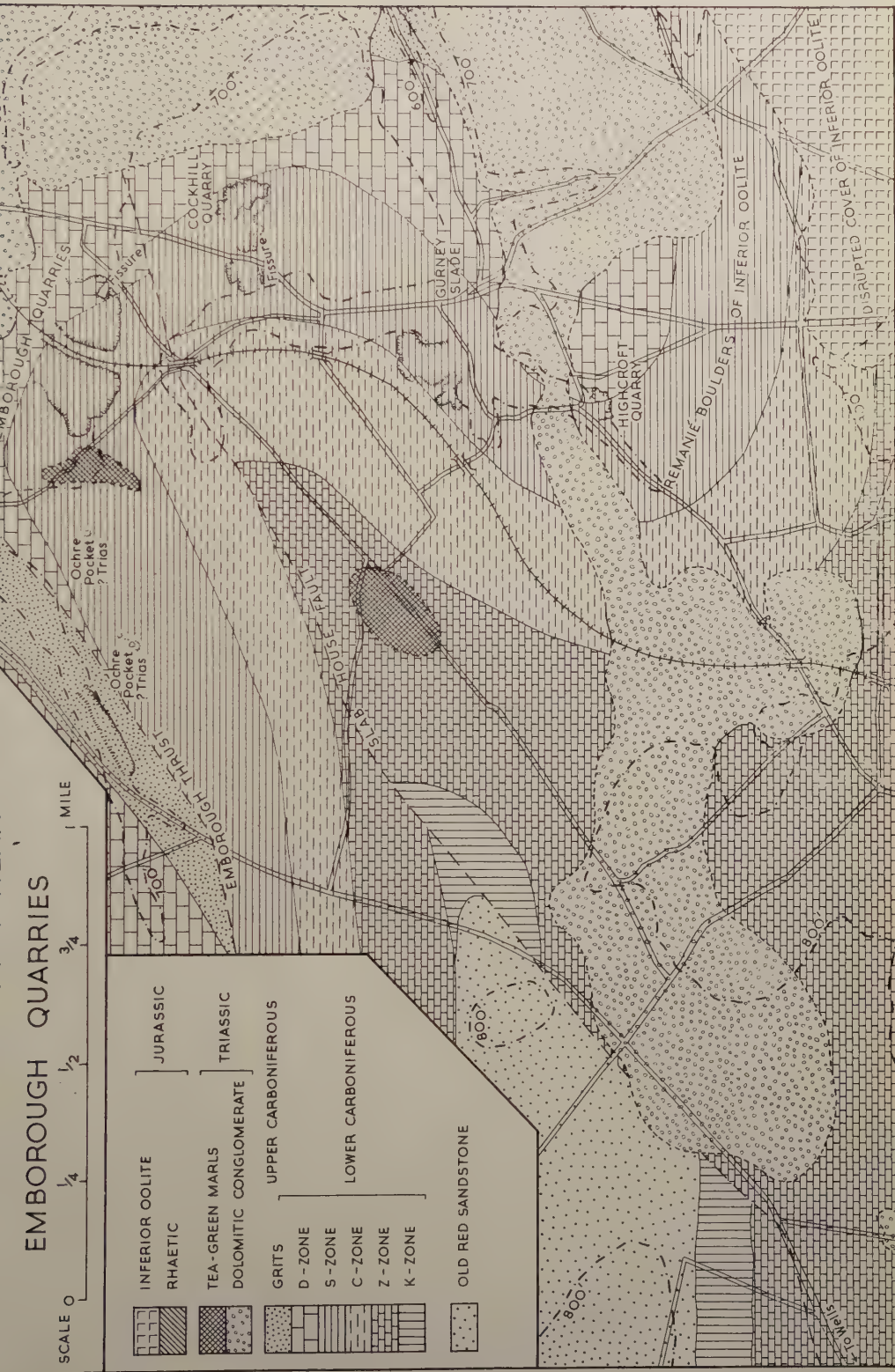


PLATE 4.—Map of the geology of the area near Emborough Quarries.

AN UNUSUAL SAUROPSID DENTITION. By PAMELA LAMPLUGH ROBINSON,
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by Professor P. B. MEDAWAR, F.R.S., F.L.S.).

(With PLATES 5-6 and 3 text-figures.)

[Read 19 January 1956.]

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INTRODUCTION.

When considering tetrapod vertebrates it is customary to regard a heterodont dentition and multicusped cheek teeth as being characteristic of mammals and some mammal-like reptiles. A few sauropsid reptiles show a slight development of accessory cusps (e.g. *Iguana*, *Chamaeleon*, some Ornithischians) but do not approach the mammalian condition in complexity of dentition. The small dentary figured on Pl. 5 appeared during the preparation of a piece of Upper Triassic fissure filling. Its dentition is so unusual compared with most fossil and recent sauropsids, that it seems to merit immediate description, even though the material available consists of two specimens only. The larger specimen is a left dentary, incomplete anteriorly (Pl. 5). The smaller one is a fragment of a second left dentary, consisting of the anterior end with part of the jaw symphysis (Pl. 6, fig. 2). The two specimens were prepared from a piece of bone-rich calcareous red silt by acetic acid, the only instrument used being a fine sable paint brush. The silt was part of the Upper Triassic filling of an underground watercourse in the Carboniferous Limestone. The watercourse is situated at Emborough Quarry, Old Down, six miles NNE. of Wells, in the Mendip Hills of Somerset. This locality is described, and the age of the watercourse sediments discussed, in the preceding paper (P. Lamplugh Robinson).

THE EMBOROUGH DENTARIES.

General Morphology.

In the larger specimen the anterior end is missing, the posterior edge is undamaged where it rises from the ventral border but is incomplete where it begins to form the coronoid process. The ventral border is extremely thin, and before being freed from the matrix it had to be reinforced along the mesial side with a fine sliver of bamboo. In the second specimen the ventral border is entire anteriorly, and so is the ventral part of the symphysis, but the latter is incomplete from a level just below the bases of the teeth.

The form of the teeth can be seen on Pl. 5 and Pl. 6, figs. 1 and 2. The number of each type of tooth present on each of the two specimens is given in the table below. Each tooth has been given a number, starting at the most anterior tooth

preserved in the specimen. A reconstruction of the whole dentary has been made (Pl. 6, fig. 1) by equating the fifth tooth of the smaller specimen with the first tooth of the larger specimen. In both specimens this is the last tooth which has a simple subconical form, and there are other points of agreement in details of shape and size of the two specimens at this position. Comparison of the two specimens shows that the number of teeth which are transitional in form from the sub-conical to the three-cusped type varies from one jaw to another.

Emborough Dentaries.

Type of Tooth	Small Specimen.		Large Specimen.	
	Tooth No.		Tooth No.	
Simple subconical	$\left\{ \begin{array}{l} 1. \\ 2. \\ 3. \\ 4. \\ 5. \end{array} \right.$	Broken off; 0.5 mm. of tooth embedded in alveolus Tip broken off in life, and then worn Recently erupted, enamel of tip unworn Slightly worn just posterior to tip Worn on tip	1.	Slightly worn on tip
Transitional to 3-cusped type, circular in section, a main central cusp flanked buccally and lingually by slight shoulders	$\left\{ \begin{array}{l} 6. \\ 7. \end{array} \right.$	Worn on tip of central cusp Tips of central and buccal cusps worn	2.	Recently erupted, enamel of tip unworn
3-cusped, small	$\left\{ \begin{array}{l} 8. \\ 9. \end{array} \right.$	Tips of all 3 cusps worn In process of eruption	3. 4.	All 3 cusps worn Recently erupted, enamel of tip unworn
3-cusped, large	$\left\{ \begin{array}{l} \\ \\ \\ \\ \\ \\ \\ \\ \end{array} \right.$		5. 6. 7. 8. 9. 10. 11.	Cracked, all 3 cusps worn All 3 cusps worn All 3 cusps worn Broken Recently erupted, cusp tip unworn All 3 cusps worn, the buccal cusp scored down its buccal side. All 3 cusps worn, the buccal cusp scored down its buccal side, the lingual cusp little worn.
3-cusped, large, but behind buccal cusp beginnings of a small accessory cusp			12.	Lingual and buccal cusps worn, central cusp with oblique wear facet on anterior side, two concave wear facets well down sides of tooth—one on anterior one on posterior side.
Central cusp largest and highest, a lingual and buccal cusp, behind buccal cusp a small accessory cusp and on posterior cingulum small denticulations			13.	Central cusp slightly worn, an oblique facet on anterior side.
			14.	In process of eruption.

Tooth wear.

The beautiful preservation of the two specimens allows wear facets to be recognized on the teeth. The form and distribution of these has been listed in the table. The more anterior cheek teeth have wear facets confined to the tips of the cusps, but posteriorly the sides of the teeth have been scored locally, particularly in the case of tooth no. 12 on the larger specimen. The latter instances suggest that the wear on the cheek teeth is probably due to occlusion with the cusps of the maxillary teeth.

Tooth implantation.

The way in which the teeth are implanted in the dentary is shown by tooth no. 1 on the smaller specimen, for this tooth has been broken off leaving the base cut across in transverse section; also by tooth no. 9 in the same specimen, and by the condition of the bases of the teeth in the larger specimen.

When fully erupted and in use the teeth lie in very shallow alveoli, to which they are firmly united by bone of attachment, the latter having a coarsely spongy or fibrous appearance. Bone of attachment sheathes the tooth above the edge of the alveolus. On both buccal and lingual sides the bone of attachment gradually loses its spongy appearance as the interstices become filled up with bone, until a fairly compact layer has been formed which is continuous with the walls of the dentary. At its upward limit the bone of attachment retains its spongy texture and appears as a ring of fibres radiating from the base of the free portion of the tooth. The upward growth of bone of attachment round the bases of the teeth makes the latter appear to be set in much deeper alveoli than is originally the case at eruption. The upper part of each side of the dentary, though apparently a continuous sheet of bone, is formed of a longitudinal series of increments of bone of attachment.

The simple conical teeth at the anterior end of the dentary are slightly pleurodont.

Tooth replacement.

The condition of tooth no. 10 on the larger specimen indicates the way in which the teeth were shed. The cusps on this tooth are heavily worn. On the lingual side an outer layer of compact bone just below the tooth has been resorbed, and a resorption aperture is visible in an inner layer of bone immediately above the base of the tooth. On the buccal side the edge of the alveolus is becoming distinct from the base of the tooth, suggesting that some absorption of bone of attachment has begun at this point. In neither specimen is there an empty alveolus.

On the smaller specimen, the last tooth preserved, no. 9, is in the process of eruption. Its crown is fully formed, the three cusps being crisp and unworn and well covered with enamel. The whole tooth is only half the height of the fully erupted teeth anterior to it, for the body of the tooth is not fully grown. The base of this tooth is attached to a thin sheet of bone, visible only on the buccal side, and in continuity with the bone of the dentary wall. On the lingual side this sheet of bone was destroyed in preparation. Spongy bone of attachment has not yet begun to form round the lower part of the tooth, and the edge of the alveolus is distinct on the lingual side.

On the larger specimen tooth no. 4 is fully erupted. Bone of attachment has begun to grow up round the base of the tooth but the edge of the alveolus is still distinct on the buccal side. On the same specimen the newly erupted tooth no. 9 shows a slightly later stage in the upgrowth of the bone of attachment. On the buccal, and particularly on the lingual, side a patch of coarse spongy bone forms an interruption to the smooth upper part of the dentary wall. Tooth no. 13 is only a little worn, and on the lingual side only a few spongy holes below its base betray the presence of its bone of attachment, which here seems to form an integral part of the upper portion of the dentary wall.

On the larger specimen teeth nos. 2, 4 and 9 are newly erupted. This suggests a fairly rapid rate of replacement. A fourteenth tooth is being added at the posterior end of the tooth row,

RELATIONSHIPS OF THE EMBOROUGH DENTARIES.

In order to discuss the systematic affinities of this reptile it is necessary to consider an Upper Triassic genus from Texas. *Trilophosaurus buettneri* was the name given by Case (1928) to a fragment of a dentary with transversely broadened teeth whose crowns bore a row of three small cusps. Later, at another locality in Texas, abundant remains of *T. buettneri* were discovered in two quarries, and J. T. Gregory was able to give a fairly complete description of the whole skeleton (Gregory, 1945). *T. buettneri* was placed in the order Protosauria, as it possesses an upper temporal fossa and seems to have been terrestrial in habit. The premaxilla is edentulous, but forms a strong bony beak, as does the anterior part of the dentary. At present, *T. buettneri* is the only known genus and species of this type of Protosaur, and it has not been found outside Texas.

Some jaws and teeth were recently found in an Upper Triassic fissure filling at Ruthin Quarry, St. Mary Hill, near Cowbridge in Glamorgan (Thomas, 1952). It will be shown that these jaws and teeth must be regarded as belonging to a new genus related to *Trilophosaurus*. In certain characters of its dentition this new genus from S. Wales is morphologically intermediate between *T. buettneri* and the heterodont reptile from Emborough. It is therefore proposed first to outline the characters of the jaws and dentition of *T. buettneri*, then to describe the new genus from South Wales, and finally, by a comparison with both these forms, to discuss the systematics of the Emborough dentaries.

Trilophosaurus buettneri Case.

"The maxillaries not only bear the teeth but also extend up on the side of the snout for some distance. Below the front of the orbit an overhanging ridge arises outside the alveolar portion and gradually widens posteriorly to a point beneath the middle of the orbit where it separates from the alveolar ramus as a distinct process articulating with the jugal."

"The alveolar ramus is heavy, deep and straight, running parallel to that of the opposite side. It bears 12 to 15 transversely broadened, sharp-edged, three-cusped teeth."

"Behind the teeth the posterior end of the maxillary is rounded and turns ventrally, overlapping the base of the lateral pterygoid flanges." (Gregory, 1945, p. 280.)

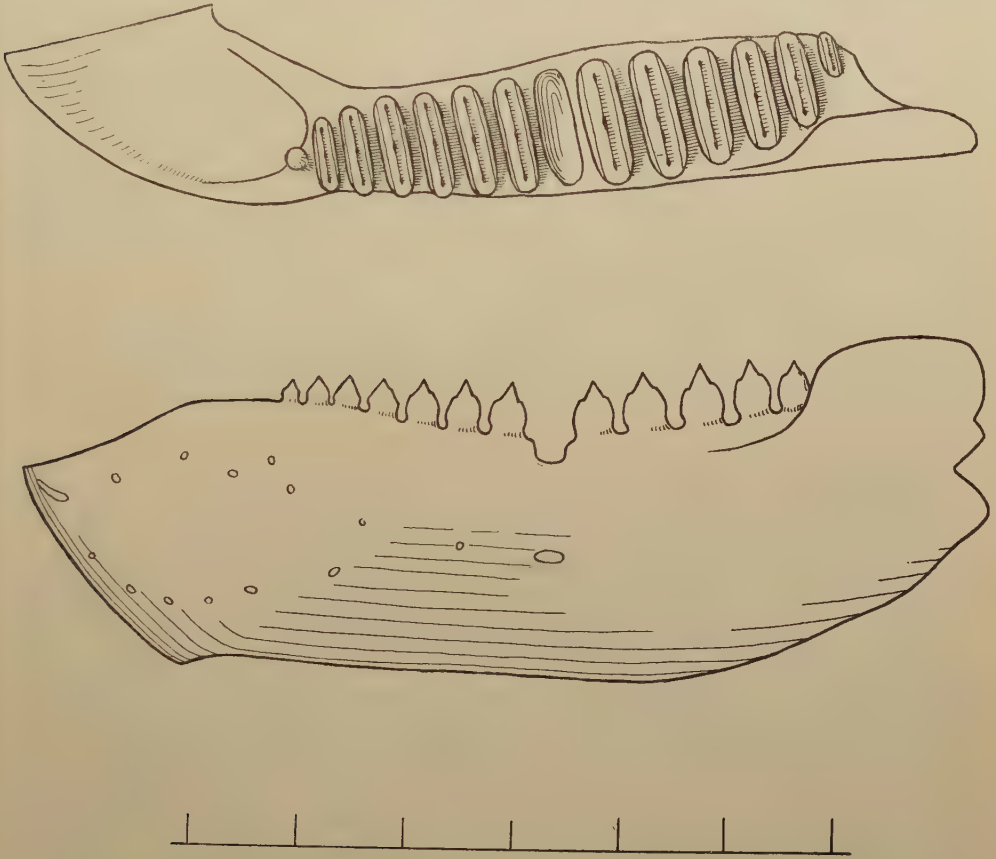
The morphology of the lateral aspect of the dentary is shown in the text-figure below (fig. 1). This figure is taken from Gregory's reconstruction of the lower jaw, given in his fig. 4, except that it has been reversed and the posterior border of the dentary has been traced from that shown in the specimen figured in his Pl. 21, fig. 3. The ventral border of the dentary is thin and sharp-edged in transverse section. The symphyseal region, as seen from above, forms a broad spoon-shape bounded laterally by the sharp-edged, edentulous, occlusal edge of the jaw.

The cheek teeth of maxillaries and dentaries are so similar that one description serves for both. There are 13 or 14 teeth in the maxilla and a modal number of 14 in the dentary. The first tooth is small, round and conical. The succeeding teeth are transversely widened and their width slowly increases posteriorly to about the 8th or 10th tooth of the maxilla and to the 10th or 11th tooth of the dentary, beyond which it decreases slightly to the penultimate. The last tooth is very small, slightly widened transversely or almost round, and its crown bears three cusps of which the central one is often larger and higher than the lateral ones. In one specimen there were two small teeth at the posterior end of the maxillaries, the penultimate transverse, the last round.

The crowns of the transversely widened teeth swell to form minute lateral, central and lingual cusps, joined by a slightly concave blade. The anterior and posterior faces of the crowns are shallowly concave as far down as the cingula. The latter are situated just above a swelling at the base of the crown and rise slightly both lingually and buccally, where they disappear into the smooth ends of the teeth,

At the base of the enamel the crown suddenly constricts and then drops straight to the alveolar border. The teeth are symmetrical to both longitudinal and transverse planes.

On Case's type fragment the largest tooth preserved is just over 4 mm. in width. Judging by its position in the tooth row it does not quite attain the maximum width possible for a jaw of this size. Gregory's specimens seem to fall into two size groups. His Quarry 2 contained small specimens only, Quarry 1 a few small ones but mainly larger sized specimens. Gregory mentions a specimen from Quarry 2 in which the maximum tooth width was 5.7 mm. The mean tooth width of the



TEXT-FIG. 1.—*Trilophosaurus buettneri* Case. Left dentary; above, crown view; below, lateral view. Scale in cm.

widest tooth in ten lower jaws from Quarry 1 was 10.5 mm. The smaller specimens have as many teeth as the larger. The length of the tooth row on both maxillaries and dentaries was 48 mm. in the larger specimens. A small lower jaw from Quarry 2 had a tooth row 24.6 mm. long.

Gregory describes the tooth implantation as thecodont. The teeth have deep open roots set in alveoli separated by thin laminae of bone, but he notes the difficulty of deciding the exact limits of jaw and tooth near the alveolar rim. "Case regarded the functional teeth as solidly grown to the borders of the alveoli in a pseudo-acrodont fashion." (Gregory, 1945, p. 292.)

"A series of fine vertical striations in the bone at the edges of the alveoli may be observed in some specimens. On the sides of corroded jaws these lines radiate outward from the ends of each tooth. The contact of tooth with bone merges in this striated zone like the infolded bases of labyrinthodont or acrodont teeth. The implantation thus appears as a combination of thecodont and acrodont types. The thecodont condition is, in *Trilophosaurus*, undoubtedly more primitive and of real systematic significance. The firm intergrowth of tooth roots and jaws may be a secondary adaptive development related to the specialized, chewing function of the teeth. It is not clear what role this condition played in the periodic shedding and replacement of the teeth." (Gregory, 1945, p. 292.)

The succession of teeth was vertical, successional teeth lying in the pulp cavities of their functional predecessors. Succession seems to have taken place in a very orderly manner along the tooth row, from front to back, the next renewal of the front teeth beginning at about the time when the last cheek tooth had been replaced. Simultaneous renewal of opposing teeth in upper and lower jaw and of the opposite teeth of each side of the mouth is indicated. No mention is made of the method of shedding the teeth, but on Gregory's Pl. 21, fig. 1, showing the mesial aspect of the lower jaw, the penultimate tooth and the three preceding ones have a small round hole below the base of each. These teeth follow a gap in the tooth row. It is possible that the holes are due to bone resorption, preparatory to shedding of these teeth.

Gregory could not distinguish any signs of wear on the crowns of the cheek teeth. The occlusion was an interlocking one, and was probably responsible for the sharp crowns always observed on unbroken specimens, for wear would be restricted to the sloping anterior and posterior sides of the crowns and tend to sharpen the edge.

The Ruthin Quarry Specimens.

The material consists of a dentary (British Museum, Natural History, R.6106), a rather battered maxilla in my own collection (P.L.R. 500), a fragment of a jaw bearing two broken and three beautifully preserved teeth (B.M., Nat. Hist., R.6107) and a jaw fragment bearing six teeth (P.L.R. 501). Cardiff Museum possesses a number of isolated teeth with well preserved crowns, and some jaw fragments which are unfortunately too waterworn to be used in description. The material was prepared by acid, but some of the matrix reacted so slowly to acetic acid that formic acid had to be used instead. Both British Museum specimens were considered to be too fragile to be freed entirely from the matrix.

The morphology of the dentary (R.6106) can be seen in fig. 2. The ventral border is thin and sharp-edged in transverse section. The anterior border is slightly damaged, but the symphysis is preserved. Figs. 1 and 2 allow the shape of the Ruthin dentary and that of *T. buettneri* to be compared. Both dentaries have an edentulous anterior region, with an occlusal ridge, and both have an ear-shaped coronoid process. The symphyseal region of *T. buettneri* is much broader transversely than that of the Ruthin dentary, and in the latter the posteroventral region is produced further posteriorly.

The maxilla (P.L.R. 500—Fig. 3) is poorly preserved posterodorsally and the anterior tip is broken. Gregory was unable to distinguish the exact course of the sutures defining the shape of the maxilla of *T. buettneri* and so gives no drawing of it. Comparison of the Ruthin maxilla with that of *T. buettneri* is therefore difficult. However the posterior end of the Ruthin maxilla is rounded and turns ventrally in the manner described for *T. buettneri* (see also internal view of the specimen of *T. buettneri* figured in Gregory's Pl. 22, fig. 2). A jugal ramus of the Ruthin maxilla is lacking but this part of the specimen is damaged, and, judging by the thickening of the maxillary wall in this region, it is not impossible that such a ramus could have been present. The dorsal ramus of the Ruthin maxilla is low in proportion to the overall length, and it seems unlikely that it extended far up the side of the snout.

The morphology of the transversely widened cheek teeth of the Ruthin specimens is best shown by R.6107 (Pl. 6, fig. 4) and by a number of isolated teeth in the Cardiff Museum collection. As a rule these cheek teeth bear a transverse row of three cusps, with a well-defined cingulum running across the anterior and posterior side of the tooth and disappearing into the tips of the buccal and lingual cusps. The cingula are located high up on the sides of the tooth. There is no trace of a sharp cutting blade between the cusps, and the latter are broadly convex. There is some variation in the size of the cusps relative to the bulk of the whole tooth, as in the penultimate tooth of the maxilla (P.L.R. 590). In maxilla and dentary all the transversely widened cheek teeth whose crowns are preserved are of the tricuspoid type. Occasionally another type of cheek tooth was developed, as seen in specimen R.6107 (Pl. 6, fig. 4). The crown of this type of tooth bore a transverse ridge, sometimes curving anteriorly at its buccal end. One or two isolated teeth of this type are to be found in the Cardiff Museum collection.



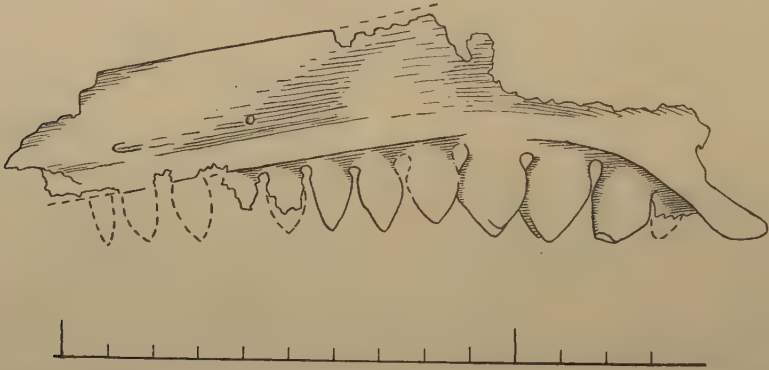
TEXT-FIG. 2.—*Tricuspisaurus thomasi* gen. et sp. nov. Left dentary ; above, crown view ; below, lateral view. Scale in mm.

The maxilla probably bore twelve teeth. The first three are broken off at the base. The first was very small, and circular in cross-section. The next two seem to have been small, transversely widened teeth. The rest were probably tricuspoid in type, although only the penultimate and the tooth anterior to it have well preserved crowns. The last tooth is broken, but was small. The largest tooth in the maxillary

now is no. 9; behind it nos. 10 and 11 are smaller, and have a different transverse alignment, their lingual ends being set more anteriorly compared with the preceding teeth.

The dentary bore nine teeth. The first two are broken off at the base, the more anterior being small and circular in cross-section, the following tooth small but transversely widened. The next four teeth are tricuspid, and gradually increase in size. Between the sixth and seventh tooth there is a large gap, triangular in shape, with the apex of the triangle directed buccally. Posterior to the gap are two tricuspid teeth, the largest in the row. The last tooth is broken off above the base, but was probably not dissimilar in form to the penultimate, though not so wide in the transverse direction. No trace could be found of a very small tooth posterior to this position.

Normally the tricuspid teeth stand upright, perpendicular to the alveolar plane of the jaw. Maxillary teeth 3 to 8 inclusive are symmetrical relative to a plane bisecting the tooth row as seen in crown view. They increase in size equally and gradually on either side of this plane, and the transverse axes of these teeth are parallel to one another and at right angles to this plane. The teeth which follow change their transverse alignment in one direction only, so that the lingual ends are gradually set more anteriorly compared with the preceding teeth. There is no trace of a sudden change in transverse alignment in the other direction, i.e. so that the buccal ends are set more anteriorly.



TEXT-FIG. 3.—*Tricuspisaurus thomasi* gen. et sp. nov. Left maxilla, lateral view. Scale in mm.

The dentary teeth 3, 4 and 5 are normal, standing upright, and having their transverse axes parallel to one another, the lingual end of each tooth being slightly anterior to the buccal end. The rest of the dentition appears to be abnormal. The sixth tooth, anterior to the triangular gap, has a slightly swollen base and leans forward at a considerable angle (fig. 2). Behind the gap the transverse alignment of the teeth shows an abrupt change in direction, the buccal ends being set more anterior than the lingual. Both of the teeth are a curious shape, particularly the seventh, which lies immediately behind the gap. Their bases are swollen, especially at the anterobuccal corner, and the teeth curve backwards and upwards, their anterior sides forming a concavity. These two teeth, and the last broken one, have a markedly pleurodont implantation on the jaw, unlike the normal anterior teeth and unlike those of any other specimen. The abnormality of the dentition centres round the triangular gap and it is possible that occlusion here with a protuberance on an abnormal maxilla has been responsible for the deformation of the teeth adjacent to the gap as they were formed and erupted, and perhaps has caused the suppression of those teeth which should fill the gap.

The form and spacing of the teeth render an interlocking occlusion impossible. Where the teeth are sufficiently well preserved to show the way in which they were worn, as in specimen R.6107 (Pl. 6, fig. 4), the areas of wear are confined to the tips of the cusps, or to the top of the ridge.

No stages of tooth replacement are visible on the specimens available. On the dentary teeth numbers 3, 4 and 5 have a zone of fibrous bone of attachment lying below their free portions, and the ventral border of each zone probably defines the true base of the tooth (fig. 2). The specimen P.L.R. 501 (Pl. 6, fig. 3), though fragmentary and a little waterworn, shows the last two teeth encircled by fibrous bone of attachment as remarked in the Emborough specimens. The other side of this specimen shows bone of attachment below the free part of the teeth in the dentary wall. The end views show how shallow in depth is the alveolar shelf on which the teeth are carried, so that there is no room for a true socket; and also demonstrate the absolute continuity of tooth wall and jaw wall in these fully erupted teeth. It seems probable that the tooth implantation of the Ruthin reptile is similar to that of the cheek teeth of the Emborough dentaries.

The length of the maxillary tooth row is 14 mm., that of the dentary 17.5 mm. The largest tooth in the maxilla measures 2 mm. across, in the dentary 4 mm. across. The size of the large dentary teeth is probably abnormal, for the largest teeth are usually 3 mm. across as in P.L.R. 501 and from measurements on the isolated teeth in the Cardiff Museum collection. The Ruthin reptile is therefore smaller than the small-sized category of *T. buettneri* specimens.

The Ruthin reptile resembles *T. buettneri* chiefly in the possession of the characteristic tricuspid cheek teeth, and an edentulous beak-like anterior portion of the jaws; also in certain minor details such as the posterior end of the maxilla and the ear-shaped coronoid process of the dentary. The similarities seem to be sufficiently close to warrant considering the Ruthin reptile to be nearly related to the genus *Trilophosaurus*. The Ruthin reptile differs from *T. buettneri* chiefly in the detailed morphology of the teeth, which lack the cutting blade of the latter, have broadly convex cusps, and must have occluded in a different way. There is also a greater variability in the form of the cheek teeth in the Ruthin specimens. Other details of shape, such as the narrow symphyseal region, and size, also distinguish the two animals. It is therefore proposed to use these differences to distinguish the Ruthin specimens as a new genus and species. The original discovery of this reptile was made by Mr. Trevor M. Thomas of Bridgend, Glamorgan, and I therefore have pleasure in naming it after him:—

Tricuspisaurus thomasi gen. et sp. nov.

The dentary R. 6106 is designated type of the new genus and species, as being the most complete specimen available, showing the edentulous character of the anterior part of the jaw. In using this type specimen the abnormal nature of the hinder part of the dentition should be borne in mind. The morphology of the cheek teeth is much more clearly shown by R. 6107 and by the Cardiff Museum specimens.

The Systematics of the Emborough Dentaries.

The type of tricuspid cheek tooth present in the genera *Trilophosaurus* and *Tricuspisaurus* is almost unique. The only other animal which possesses teeth which are remotely similar is *Diadectes*. Although Diadectid cheek teeth are transversely widened and bear three cusps they are in fact very different from those of *Trilophosaurus* and *Tricuspisaurus*, so much so that when Professor Case described the original fragment of the jaw of *T. buettneri* he referred it to the Procolophonidae and not to the Diadectidae. In the Diadectid cheek tooth the central cusp dominates the crown, standing much higher than the lateral ones; there is no cingulum; the teeth have deep roots housed in permanent sockets in the jaw bones (Watson, 1954); and they are worn in quite a different manner, by propalinal movements of the jaw.

In view of the fact that the Trilophosaurid cheek tooth is unique and characteristic it seems safe to conclude that the Emborough dentaries are those of a form related

to this genus. The majority of the cheek teeth on the Emborough dentaries bear a transverse row of three cusps, broadly convex as are those of *Tricuspisaurus thomasi*, but with much less well-developed cingula. The fact that the Emborough dentaries possess, not an edentulous beak, but a series of simple subconical anterior teeth, at once serves to distinguish them from the other two *Trilophosaurid* genera, and will be made the basis of a generic distinction. The Emborough dentaries are therefore named as a new genus related to *Trilophosaurus* :—

* *Variodens inopinatus* gen. et sp. nov.

The larger of the two specimens of *V. inopinatus* is designated type specimen.

A consideration of the functional significance of the teeth will not be attempted here. It is hoped that further material of this reptile may be obtained from the Emborough Quarry fissure filling and allow the dentition to be discussed in relation to the functional anatomy of the skeleton.

ACKNOWLEDGMENTS.

I am indebted to the authorities of the British Museum (Natural History) for permission to borrow and study their specimens from Ruthin Quarry collected by Dr. W. G. Kühne; also to the National Museum of Wales, Cardiff, for sending me their material from this locality, collected by Mr. T. M. Thomas. I should like to thank Professor D. M. S. Watson for advice and helpful discussions during the preparation of this paper, and Professor P. B. Medawar for reading the paper in manuscript.

SUMMARY.

A small sauropsid dentary from Emborough Quarry, Somerset, of Upper Triassic age, and with an unusual dentition, is described. The dentition is heterodont, with simple conical anterior teeth and transversely broadened cheek teeth which are tricuspid or multicuspid. The jaws of another reptile from Ruthin Quarry, Glamorgan, also of Upper Triassic age, are also described. This second reptile has transversely broadened tricuspid cheek teeth, the anterior part of the jaws forming an edentulous beak. Both reptiles are shown to be related to *Trilophosaurus buettneri* Case, but generically distinct. The new reptiles are named *Variodens inopinatus* gen. et sp. nov. (Emborough specimens) and *Tricuspisaurus thomasi* gen. et sp. nov. (Ruthin specimens).

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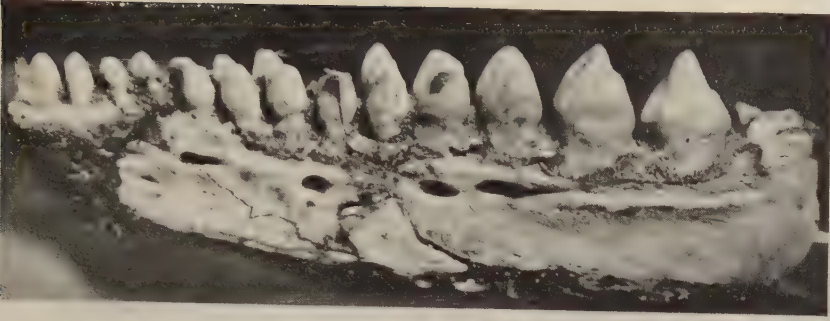
EXPLANATION OF THE PLATES.

PLATE 5.

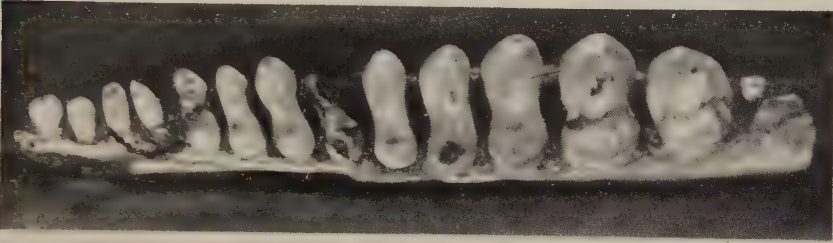
Variodens inopinatus gen. et sp. nov. Left dentary, incomplete anteriorly. Type specimen. Scale in mm.

- A. Lateral view.
- B. Slightly oblique (lateral) crown view.
- C. Mesial view, photograph reversed.
- D. Mesially oblique crown view, photograph reversed.

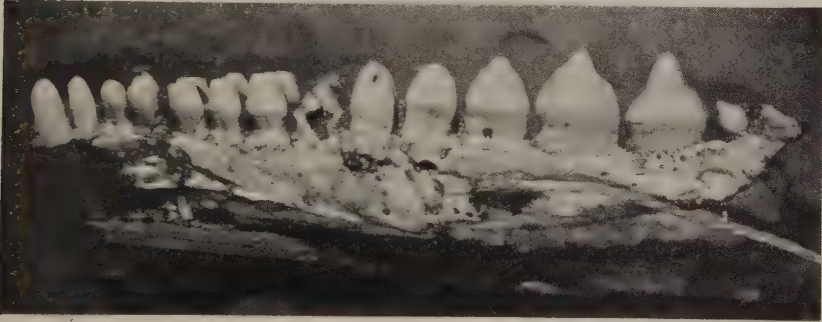
* *Trans.* Unexpected varied teeth.



A



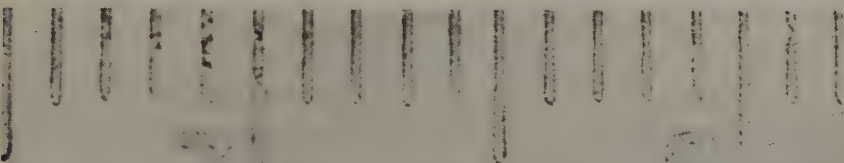
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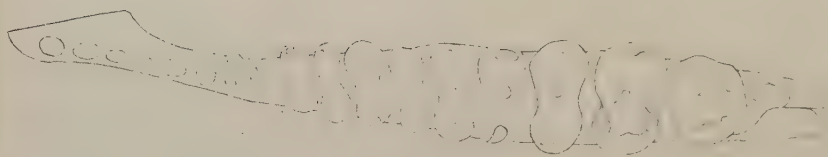
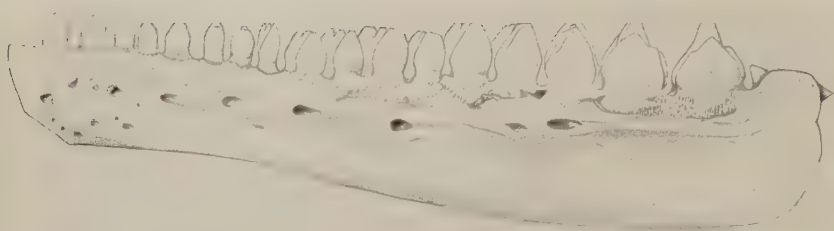


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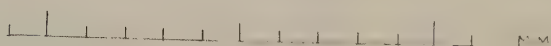


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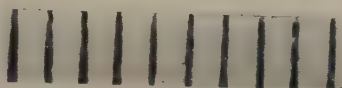
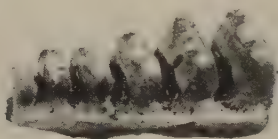


SCALE



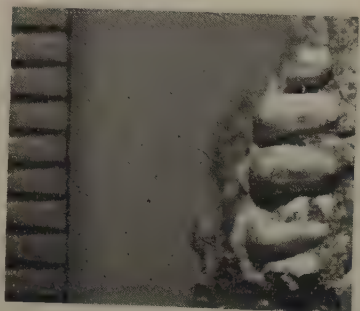
MM

1



3

2



4

FIGS. 1 & 2.—*Variodens inopinatus* gen. et sp. nov.
 FIGS. 3 & 4.—*Tricuspisaurus thomasi* gen. et sp. nov.

PLATE 6.

- FIG. 1.—Reconstruction of dentary of *Variodens inopinatus* from type specimen and paratype, locality Emborough Quarry, Somerset. Above, lateral view. Below, dorsal view (outline). Scale in mm.
- FIG. 2.—*Variodens inopinatus* paratype. Above, dorsal view, anterior end on left. Below, lateral view, anterior end on left. Scale in mm.
- FIG. 3.—*Tricuspisaurus thomasi* gen. et sp. nov. Specimen P.L.R. 501. Oblique crown view to show fibrous bone of attachment radiating from the base of the free portion of the tooth. Scale in mm.
- FIG. 4.—*Tricuspisaurus thomasi* gen. et sp. nov. Specimen B.M. Nat. Hist. R. 6107. Crown view to show morphology of tricuspid and ridged tooth crowns. Wear facets are visible on the tips of the cusps and the top of the ridge. Scale in mm.

NOTES ON THE HYDROZOA OF THE NORFOLK COAST. By RICHARD HAMOND. (Communicated by Dr. A. TINDELL HOPWOOD, F.L.S.)

(With Pl. 7 and 26 text-figures.)

[Read 21 April 1955.]

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1. INTRODUCTION.

The following notes are based entirely upon the author's own records, from December 1949 onwards, of hydroids (and of other marine animals) collected at various places on the North Norfolk coast. Although a detailed description of grounds would be out of place, the general littoral substratum is of sand and mud, often mixed, and backed by salt-marshes, the latter intersected with large drains (creeks) in which the substratum is mud and *Fucus*-covered stones. The coastline is continually altering (Steers, 1951) and with few exceptions the littoral zone is exceedingly exposed. For some miles out from the coast the sea is very shallow and the bottom highly diversified; hydroids (*Nemertesia*, *Sertularia* and *Hydrallmania*) and branching polyzoa grow plentifully on the shelly, stony and sandy patches, while on the rather thick clayey mud which occurs in places the whelk, *Buccinum undatum*, swarms in great numbers and forms the object of an important local fishery based on Wells-on-Sea. Farther east, off Sheringham and Cromer, the sea-floor is rocky and harbours crabs and lobsters; the rocks extend on to the shore only at West Runton, where within a few acres is one of the richest shore grounds in Norfolk. Finally, at Hunstanton there are large mussel-beds on the 'corner of Norfolk' from which a rich fauna can be gathered at low water in spite of the exposed situation; and any violent gale, from whatever quarter, throws ashore large masses of hydroids and other animals on to the beds, locally termed 'mussel-lays'.

The sixty-three hydroids are nearly all well-known British forms; but only twenty-seven were known from Norfolk previously, mostly from Garstang (1900) and a few each from Hincks (1868), Serventy (1934) and Gilson, Hollick & Pantin, (1944). The other thirty-six are marked with an asterisk to denote the first Norfolk Record; three of them have two asterisks and are new to the British fauna. I have not succeeded in finding several species (see Section (b) (i)) recorded by the above workers.

ACKNOWLEDGMENTS.

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2. (a) LIST OF THE NORFOLK HYDROIDS, WITH SYSTEMATIC AND BIOLOGICAL OBSERVATIONS.

Suborder ANTHOMEDUSAE (ATHECATA, GYMNOBLASTEAE).

Fam. CLAVIDAE.

**Clava multicornis* (Forskål). *Clavid, g. & sp. indet.

Fam. BOUGAINVILLIIDAE.

**Trichydra pudica* T. S. Wright. *Hydractinia echinata* (Fleming). **Bougainvillia ramosa* (van Beneden). *Bimeria vestita* T. S. Wright. **Garveia nutans* T. S. Wright.

Fam. CORYNIDAE.

Coryne muscoides (L.). **Coryne eximia* (Allman). **Coryne tubulosa* (M. Sars).

Fam. TUBULARIIDAE.

Tubularia larynx Ellis & Solander. *Tubularia indivisa* (L.).

Fam. EUDENDRIIDAE.

**Eudendrium rameum* (Pallas). **Eudendrium ramosum* (L.). **Eudendrium arbusculum* T. S. Wright.

Suborder LEPTOMEDUSAE (THECAPHORA, CALYPTOBLASTEAE).

Fam. HALECIIDAE.

Halecium halecinum (L.). *Halecium beani* (Johnston). **Halecium lankesteri* (Bourne). **Halecium muricatum* (Ellis & Solander). ***Halecium undulatum* Billard.

Fam. LAFOEIDAE.

**Lafoea dumosa* (Fleming). *Fillellum serpens* (Hassall).

Fam. CAMPANULINIDAE.

**Cuspidella* sp. cf. *costata* Hincks. *Calycella syringa* (L.). **Calycella hispida* (Nutting). *Calycellid, g. & sp. indet. **Lovenella clausa* (Lovén). **Phialella quadrata* (Forbes). **Opercularella lacerata* (Johnston).

Fam. CAMPANULARIIDAE.

Campanularia volubilis* (L.). **Campanularia integra* MacGillivray. *Campanularia verticillata* (L.). *Clytia johnstoni* (Alder). *Laomedea geniculata* (L.). **Laomedea longissima* (Pallas). *Laomedea dichotoma* (L.). *Laomedea bicuspidata* (Clarke).

Laomedea gelatinosa (Pallas). *Laomedea loveni* Allman. **Laomedea hyalina* (Hincks). **Laomedea neglecta* Alder. ***Laomedea conferta* (Hartlaub). *Laomedea flexuosa* Hincks.

Fam. SERTULARIIDAE.

**Sertularella rugosa* (Gray). *Sertularella polyzonias* (L.). **Sertularella mediterranea* Hartlaub. *Abietinaria abietina* (L.). *Abietinaria filicula* (Ellis & Solander). **Diphasia rosacea* (L.). *Diphasia attenuata* (Hincks). **Dynamena pumila* (L.). *Sertularia gracilis* Hassall. *Sertularia cupressina* L. **Amphisbetia operculata* (L.). *Hydrallmania falcata* (L.). **Thuiaria thuja* (L.).

Fam. PLUMULARIIDAE.

Kirchenpaueria pinnata (L.). *Plumularia setacea* (Ellis & Solander). **Plumularia allenii* Nutting. **Plumularia halecioides* Alder. **Plumularia diaphana* (Heller). *Nemertesia antennina* (L.). *Nemertesia ramosa* (Lamouroux).

Clava multicornis (Forskål). Occurs in Morston Creek and other creeks adjoining it, from March to June, under shells and pieces of waterlogged wood, rarely on algae. A single colony was taken on the mussel-lays in the bottom of the Harbour, 24. v. 1950, very late for this species and very low down on the shore.

Clavid, gen. & sp. indet. (Pl. 7). This occurred as a sterile colony upon the hydrocaulus of a large *Laomedea hyalina* (q.v.), cast up in Blakeney Harbour, 23. ix. 1950; the colony was kept alive for a short time but gonophores were not developed, and the polyps were mounted as a slide. The following is a description of them :

From a creeping filiform stolon there arise singly at intervals the polyps, which are somewhat fusiform, with a bluntly-rounded hypostome and about twelve filiform tentacles scattered evenly over the middle third of the polyp. The detailed structure is characteristic, since the mesoglea is a uniformly thin sheet throughout, the ectoderm being composed of a single layer of polygonal cells which are somewhat thicker around the tentacle-bearing region; but the endoderm, although thin in the lower part of the polyp, rapidly becomes thicker going upwards and hence widens inwards uniformly until, at the level where the hypostome shades off into the mid-region of the polyp, the coelenteron has dwindled to a mere channel. Tentacles up to three or four times the length of the polyp itself, exceedingly slender, filiform, with nematocysts arranged in elongated clusters, of from thirty to fifty, which often take on an irregularly subspiral arrangement; the clusters are larger and more numerous towards the distal end of the tentacle, though even here they never coalesce.

Trichydra pudica T. S. Wright. Three polyps, agreeing closely with the published descriptions and figures of this species (Hincks, 1868; Rees, 1941) were seen expanded on one side of the test of a tunicate (*Microcosmus claudicans* (Savigny)), upon a living *Buccinum undatum* taken at 53° 09' N., 01° 05' E., 13. v. 1954. It has been suggested (Rees, 1941; Russell, 1953) that the medusa of *T. pudica* may be *Lizzia blondina* Forbes, which I have never taken here although a closely allied species (*Rathkea octopunctata* (M. Sars)) occurs commonly in spring and is dealt with below.

Hydractinia echinata (Fleming). Common at low water among the mussels in Blakeney Harbour, always on shells with *Eupagurus bernhardus*, and occasionally at sea, in whelk-pots, e.g. about nine miles N. of Stiffkey, 53° 06' N., 00° 58' E., 27. ix. 1951. I have also seen it on *Natica* with *Eupagurus*, 54° 28' N., 01° 35' E., 30. iv. 1950, rather more than half-way from here to the Dogger Bank; and on the inside of an old *Cardium* shell from about 40 miles farther east. Breeding on the Norfolk coast takes place all the year round but mostly in the summer, and it is very unusual to find a completely sterile colony.



Clavid, gen. et sp. indet. For full description see p. 296, opposite.

(Photograph by H. R. Hewer; ectoderm of head of polyp slightly retouched and background fog removed chemically to bring out three of the tentacles which are out of focus.)

Bougainvillia ramosa (van Beneden). Near the coast the most usual form of colony is coarsely pinnate (fig. 2) and about 40 mm. high, often less; this is generally distributed, but a rather distinctive small form (fig. 1) occurs abundantly at Hunstanton and rarely elsewhere. I have never seen medusa buds on normal colonies of the same size as the small form, but the young medusae from each were released in August and September 1952, and both agree exactly with Hincks's drawing (1868, pl. XIX, fig. 2c). Between tidemarks tiny hydroids resembling *B. ramosa* are often found but so far have not been reared successfully.

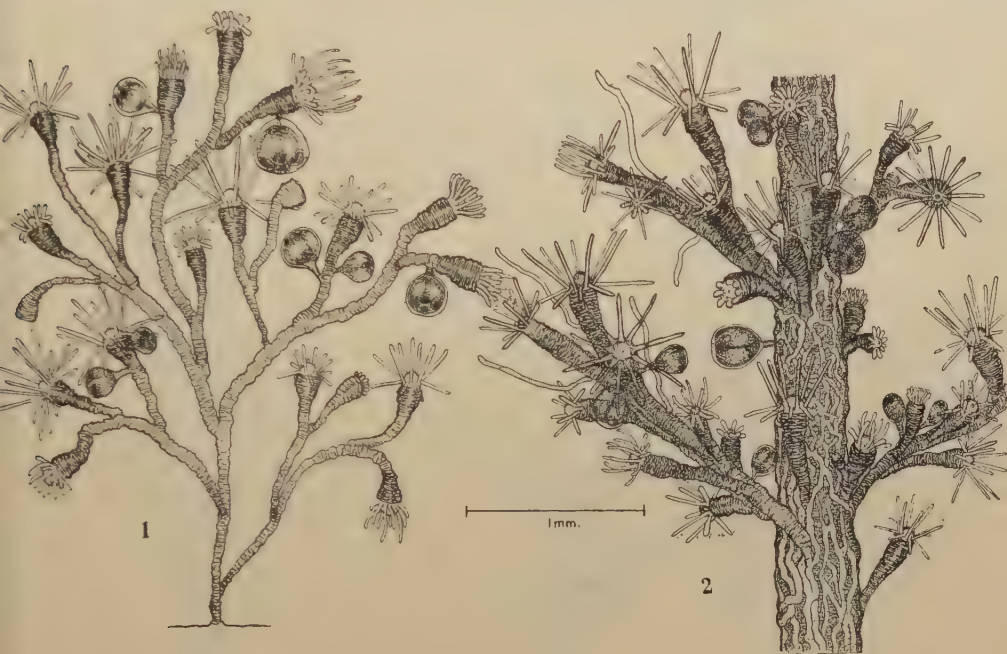


FIG. 1.—*Bougainvillia ramosa* (van Beneden); small form with medusa-buds, Hunstanton, 5. ix. 1952.

FIG. 2.—*B. ramosa*; large pinnate colony with medusa-buds, 53° 09' N., 01° 01' E., 25. viii. 1952.

Bimeria vestita T. S. Wright. An interesting little hydroid, previously known locally only from off Yarmouth (Garstang, 1900), of which I collected many fertile colonies on the shore at Hunstanton, 16. vii. 1953, growing all up and down the stem of a dead *Hydrallmania* (fig. 4); they corresponded well with Hincks's description and figures (1868). A portion of a similar colony from Lowestoft is shown in fig. 3. Except that it produces medusae, *Thamnostoma russelli* Rees (1938) is precisely like my colonies of *Bimeria*, though for the moment it will be best to keep them generically separate as our knowledge of these forms is very insufficient.

Garveia nutans T. S. Wright. This has occurred only a few times, and always sterile, on *Tubularia indivisa*: 28. ii. 1950 at Hunstanton; 5. iii. 1950 in Blakeney Harbour; 1. vii. 1950 at 53° 11' N., 00° 57' E., off Wells; 23. iii. 1952 at Hunstanton. A colony taken at 53° 31' N., 01° 41' E., 5. v. 1950 ("Romilly") was much branched and had several well-developed gonophores.

Coryne muscoides (L.). In summer, this is very abundant at West Runton at the same level as the alga *Corallina*, fringing little pools below the water level.



FIG. 3.—*Bimeria vestita* Wright. Dead colony on *Hydrallmania*. The glove-like pseudohydrotheca can still be seen. Lowestoft Harbour, 21. viii. 1950.

FIG. 4.—*Bimeria vestita* Wright. Male gonophores continuing their development on an otherwise dead colony, Hunstanton, 16. vii. 1953.

I have also found it a few times cast up at Hunstanton, usually on *Hydrallmania*; and growing in the lowest reaches of Blakeney Harbour or cast up there upon larger hydroids. Out at sea, I have found it as follows:

- 1½ miles north of Cley beach, on *Hyas araneus*, 2. i. 1951.
- 53° 10' N., 01° 10' E., on *Hydrallmania*, 2. vii. 1951.
- 53° 12' N., 01° 08' E., on *Hydrallmania*, 20. viii. 1951.
- 53° 08' N., 01° 05' E., on *Flustra foliacea*, 12. ix. 1951.
- 53° 06' N., 00° 58' E., on floating corks, 27. ix. 1951.

Coryne eximia Allman. Fertile colonies, forming blood-red mossy tufts upon *Abietinaria abietina*, were trawled in May south-west of the Dogger Bank ("Romilly") but in Norfolk waters the colonies are large and much branched with horny stems becoming pale lemon-yellow above, the coenosarc being of an ochreous or ginger

shade and the polyps mustard-yellow with a trace of pink: the polyps near the apices of the branches were sterile, while those half-way up the colony bore clusters of pink medusa-buds, each with four red tentacle-bulbs having a dark brown ocellus. A colony of this type, collected at low water on the "Iron Steamship" on 10. vi. 1952, released, three or four days later, some young medusae which were identified as *Sarsia eximia*. Other large specimens have been collected by me ($53^{\circ} 10' N.$, $01^{\circ} 18' E.$, 17. vii. 1950, and $53^{\circ} 08' N.$, $01^{\circ} 05' E.$, 12. ix. 1951, both with medusa-buds, on corks) while small sterile colonies are often thrown ashore among masses of hydroids.

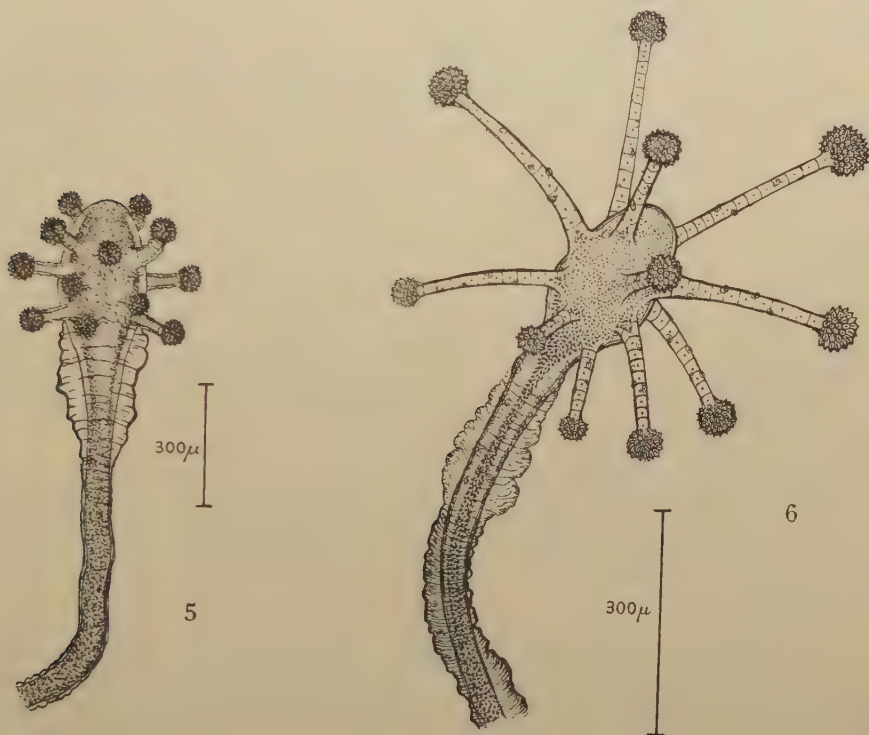


FIG. 5.—*Coryne tubulosa* (M. Sars). On *Scrupocellaria reptans* upon *Flustra foliacea*, cast up in Blakeney Harbour, 25. xii. 1949.

FIG. 6.—*C. tubulosa*, from a creek in the marshes, Blakeney Harbour, with thickened ectodermal ring at upper margin of pseudohydrotheca. 15. iii. 1951.

Coryne tubulosa (M. Sars, 1835) syn. *C. sarsi* (Lovén, 1836). Unlike *eximia*, this species is locally frequent in spring between tidemarks among algae and polyzoans. The hydrocauli are usually single, but sometimes branch. South-west of the Dogger Bank I found a fertile colony in May ("Romilly"), but locally the breeding season is earlier. On 27. ii. 1954, at Hunstanton, I found a small colony of *C. tubulosa* cast ashore on *A. filicula*; this colony was kept alive and by 21 March had produced many medusa-buds, some of which degenerated; all the polyps were resorbed before the release of one young medusa on 5 April, three more on 14 and yet another on 15 April. At once small polyps began to arise and by 25 April were carrying medusa-buds which later degenerated. In early June the experiment was concluded.

Meanwhile, young medusae of comparable age were taken locally in the plankton, one on 19. iv. 1954 and four more three days later, all of which (as well as those in the laboratory) agreed closely with the description in Russell (1953). An apparently precisely similar *Coryne* found in Morston Creek on 18. ii. 1954 was kept in the same dish as the Hunstanton colony and never produced medusae until discarded with the other in June. A constant feature in *tubulosa* is an ectodermal thickening (fig. 6) around the polyp at the upper margin of the pseudohydrotheca; in fig. 5 is shown a polyp with an abnormally large pseudohydrotheca.

Tubularia larynx Ellis & Solander. Abundant out at sea on old corks, also in the "Iron Steamship" and on "Saint Guenowle". Fertile colonies occur locally throughout the summer.

Tubularia indivisa (L.). This beautiful hydroid, famous for its robust growth and lovely colouring, is quite common out at sea and is occasionally cast ashore. As in *larynx*, breeding takes place in the summer. The stiff straw-like hydrocauli often have smaller epizoid forms growing on them, and a fine cluster will harbour the nudibranch *Cuthona aurantia*. In deep water, e.g. 50 fathoms, it grows much larger than in lesser depths near the coast. It is known to be generally distributed in the North Sea (Hincks, 1868; also personal observations).

Eudendrium rameum (Pallas). Occurs not very commonly all along the Norfolk coast a little way offshore. Breeding season November–March; the ova are clustered in groups of from four to ten upon branchlets arising from the main stems and principal branches. Development as in *E. arbusculum* (q.v.), but with total atrophy of the female polyp. The sterile polyps are large, with chestnut entera and transparent tentacles. The growth is especially treelike, and less bushy than that of *arbusculum*.

Eudendrium ramosum (L.). This is about as common as *E. rameum* throughout the year, but all the Norfolk specimens seen so far have been sterile: colonies trawled by the "Romilly" between here and the Dogger Bank were breeding in May. From the other species of *Eudendrium* which occur here the pinnate growth clearly distinguishes it.

Eudendrium arbusculum T. S. Wright. Common on whelk-tows, corks and buoys out at sea, and flourishes throughout the summer. While in 1952 there was hardly any, in 1951 the species was exceedingly abundant, and the year before that moderately common (few observations). In June and July 1951, I took fertile specimens, shown in figs. 7 and 8. My colonies agree closely with Hincks's account (1868) except for the following details: the abdominal belt of nematocysts is constantly present, but the polyps are rose or chestnut with colourless tentacles (cf. Hincks's 'snowy polypites'); the male gonophores are borne upon a perfect polyp, whereas Hincks implies that the polyp is atrophied ("male gonophores borne in clusters on short stems"); the female polyps (unknown to Hincks or to Broch (1916)) never quite dwindle to blastostyles but retain a hypostome surrounded by about half the usual complement of tentacles, even when bearing six or seven contemporary spadices, each hooked in the form of a question mark around a single ovum. The outside of the spadix is carpeted with large nematocysts similar to those found around the base of the polyp. Only when the complete set of ova has developed some little while does the polyp with its spadices become partially resorbed, leaving as many embryos as there were spadices, each encased in a very thin envelope of perisarc. Immediately after this a new polyp grows up, with consequent elongation of the perisarc of the hydrocaulus, and produces a batch of ova in its own turn; this stage is shown in fig. 8, where the ova are still young and the polyp fully developed.

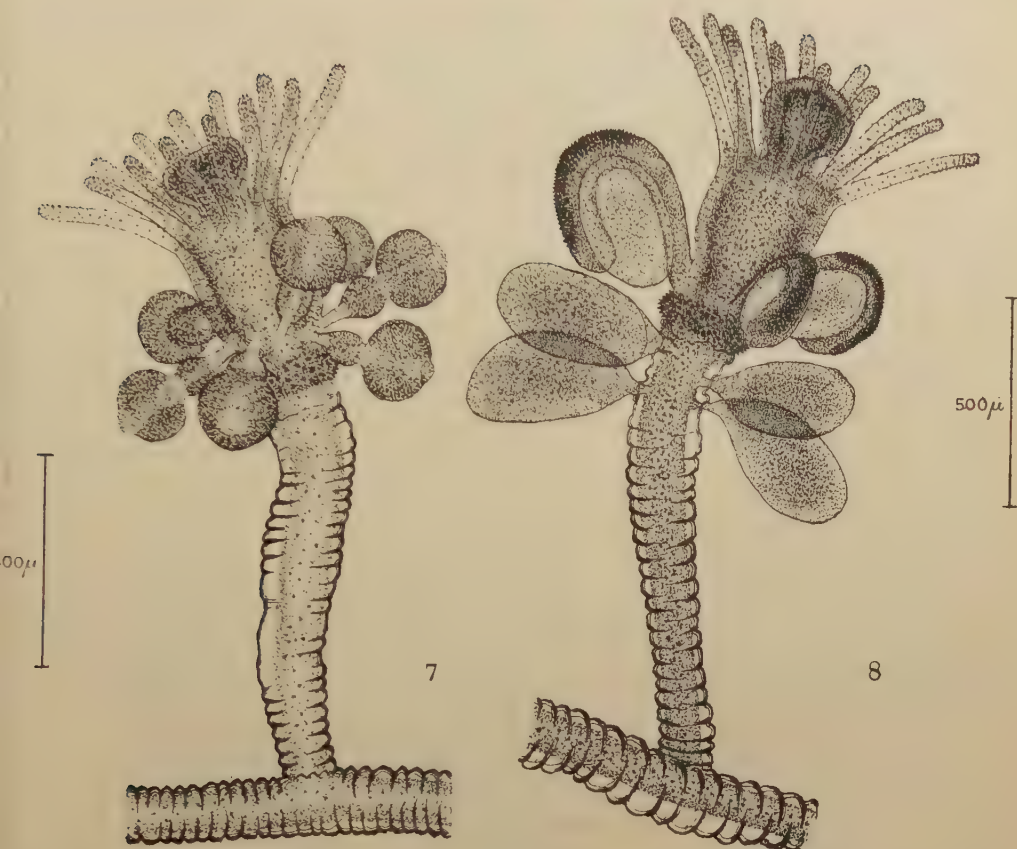


FIG. 7.—*Eudendrium arbusculum* Wright. Male polyp, with numerous spadices, each having two or three testes of which the largest and most distal is mature without atrophy of the polyp. 53° 05' N., 01° 10' E., 16. vi. 1951.

FIG 8.—*E. arbusculum*. Female polyp, taken with the last (on another colony), whose structure is described in the text. Notice the frosted carpet of large nematocysts on the outside of each spadix as well as round the base of the polyp, also the successive generations of embryos.

Order LEPTOMEDUSAE (THECAPHORA).

Halecium halecinum (L.). Occurs offshore very commonly but never grows very large locally. Breeding from April to July; the large non-retractile hydranths are frequently attacked by nudibranchs to which they fall an easy prey, though curiously enough *Doto coronata* is much more abundant on *Sertularia cupressina* whose polyps are small and retractile.

Halecium beani (Johnston). Compared with the last species, this hydroid is very often epizoid upon larger forms (especially *Hydrallmania*; rarely on *H. halecinum*) and hence more often cast ashore; the growth is far more bushy and the coenosarc milky-grey rather than yellow. For the difference between *H. beani* and *H. lankesteri* see the latter. In Norfolk waters *H. beani* breeds from April to July.

Halecium lankesteri (Bourne) syn. *Halecium robustum* Pieper (1884), *Haloikema lankesteri* Bourne (1890). This species is one of a number that have been called '*Halecium robustum*' from time to time; the name '*robustum*' should, however, belong to the first to receive it, *Halecium robustum* Verrill (1873) (see Totton, 1930). It may be helpful to indicate the position with regard to the other species, which have been called '*robustum*' :

Former name	New name	Authority
<i>Halecium robustum</i> Pieper (1884)	<i>H. Lankesteri</i> (Bourne, 1890)	Bedot (1914)
<i>H. robustum</i> Allman (1888)	<i>Ophiodissa arborea</i> (Allman, 1888)	{ Allman (1888) Bedot (1925)
<i>H. robustum</i> Ritchie (1907)	<i>Ophiodissa arborea</i> (Allman, 1888)	Bedot (1925)
<i>H. robustum</i> Ritchie (1911)	<i>H. macrocephalum</i> Allman (1888)	Ritchie (1913)
<i>H. robustum</i> Vanhöffen (1910)	<i>Ophiodissa arborea</i> (Allman, 1888)	Ritchie (1913)
<i>H. robustum</i> Motz-Kossowska (1911)	<i>H. petrosum</i> Stetchow (1919)	Stechow (1919)
<i>H. robustum</i> Nutting (1901)	<i>H. harrimani</i> Nutting (1901)	Nutting (1901)

Of all these species, only *Halecium lankesteri* is British. *H. petrosum* occurs in the Mediterranean, and the others farther afield.

It is a curious fact, that few of these species mis-named '*robustum*' actually bear any close resemblance to one another; the explanation is rather that '*robustum*' is a generally appropriate name for many Haleciids with their handsome rugged growth, and has been independently employed by several authors who had failed to consult the relevant literature before doing so, though in two instances, Allman (1888) and Nutting (1901), the mistake was rectified by the authors themselves.



FIG. 9.—*Halecium lankesteri* (Bourne). Small sterile colony, cast ashore alive upon *Delesseria*, Blakeney Harbour, summer 1950.

Among the other British species, *H. lankesteri* most resembles small colonies of *H. beani*; it is, however, quite distinct (Babic, 1913; Bedot, 1914) and I have never seen any intermediates. Hincks's (1868) account contains nothing which might show that he had ever seen *H. lankesteri* or confused it with *H. beani*; but

I have seen a specimen of *H. lankesteri* collected in 1872 from 50° 00' N., 02° 00' W., that is, in the channel between Cherbourg and the Dorset coast, upon *Nemertesia antennina*. It appears to be a lusitanian species which at the present time seems to have established a fairly secure residence in this country. Recently (26. vi. 1952) magnificent colonies of both sexes, with gonophores, were collected in the "Iron Steamship" and this description is largely based upon them:

Colonies arising from a creeping filiform branched stolon running over red algae, hydroids or large polyzoa. Hydrocaulus monosiphonic, much branched to form bushes about 20 mm. high; branches diverging only slightly from the main stem, and themselves branching in many places. Internodes all remarkably alike, being straight and with the broad and shallow hydrophore projecting well out; coming up to it from below, the internode wall has a sharp concave sweep outwards. Opposite the hydrophore the next internode arises, and is sharply crooked upwards so as to ascend parallel to the one from which it sprang; these joints are slightly wrinkled (the rest of the internode being smooth), and their form is the most

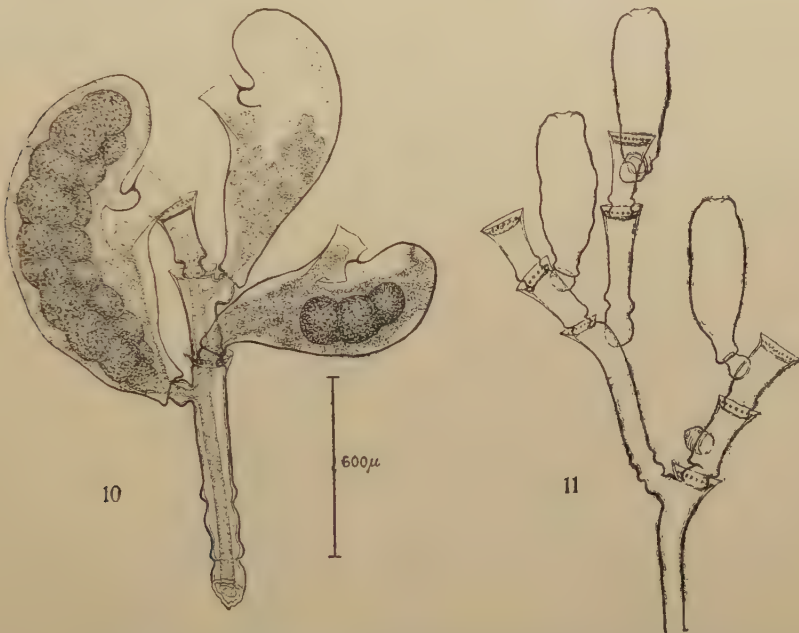


FIG. 10.—*H. lankesteri*. Female gonothecae on dead colonies, with developing ova.

FIG. 11.—*H. lankesteri*. Empty male gonothecae.
Both these were collected with that shown in fig. 9.

characteristic feature by which to tell *lankesteri* from the preceding species. The hydrothecae themselves are like those of *beani*. The polyps are about as long as the internodes, with 20–24 tentacles in one whorl held alternately raised and depressed (though this posture is not quite constant, nor regular). The gonophores are borne on the lower part of the colony (but not on the hydrorhiza) upon special branchlets which have shorter internodes with many wrinkles, and are held more fanwise than the ordinary branches and have only one or two polyps if any. The male gonothecae (fig. 11) are simply sausage-shaped, about twice the length of an internode, or less; females (fig. 10) larger, like those of *beani* but broader across, very incurved and smooth, with a short wide tubular opening on the inner side of the curve which is inclined upwards at about 45° and has two polyps issuing out

of it. In both sexes the footstalk is more or less sharply curved so that the gonophore stands vertically; where two occur together one arises from the side of the hydrotheca and the other actually comes out of it (as already noted by Bedot). I have seen colonies (all unpublished so far) from the following localities:

Plymouth Breakwater (coll. P. L. Kramp, 1914), Studland Bay, Dorset (B.M. 90.7.22.5), Mawganporth, North Cornwall (coll. L. W. Mullinger, 1951), and at Skokholm Island in South Wales, collected by myself in August 1951. Small colonies are abundant on the roots of *Bugula plumosa* at West Runton and at Hunstanton; while in Blakeney Harbour it has occurred many times.

Halecium muricatum (Ellis & Solander). Fertile colonies have not yet been seen, but it occurs regularly in small numbers, mostly on *Hyas araneus*, on the whelk-grounds off Sheringham and Wells. The Norfolk specimens are only 4 cm. high; farther out they are much larger; the "Romilly" trawled colonies 13 cm. high on the Dogger Bank.

Halecium undulatum Billard. This was first described in 1921 from two small colonies taken off the Belgian coast. As will be shown below, it is really much more widely distributed, but has frequently been confused with *Halecium tenellum* Hincks.

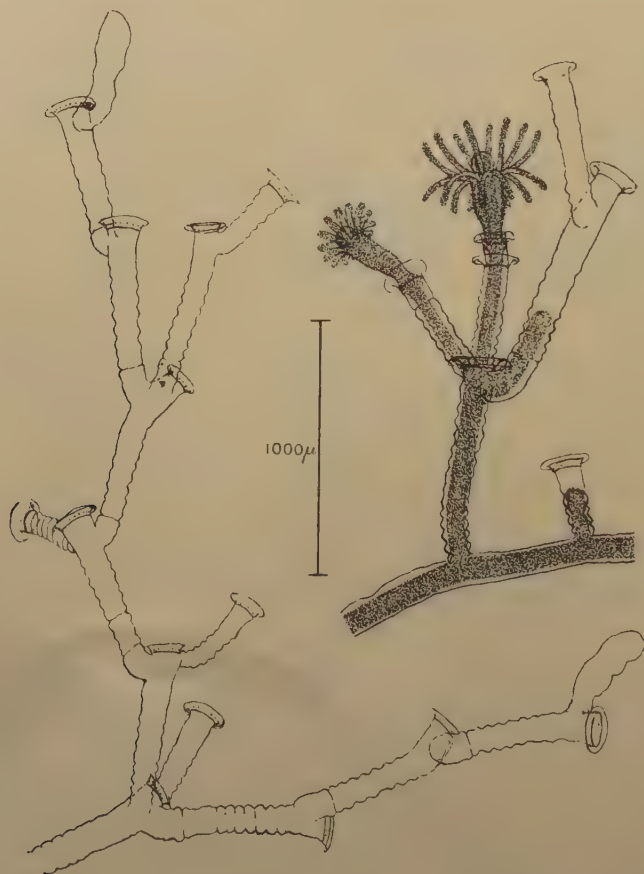


FIG. 12.—*Halecium undulatum* Billard; part of a small colony from 53° 05' N., 01° 01' E., 16. vi. 1951. The colonies may be slenderer than this, or (less often) stouter.

The specimens I have seen differ in certain points from those described by Billard, and although I regard them as conspecific (unfortunately I have not seen the types) a complete description of my own specimens (figs. 12, 13) follows:

A small *Halecium*, whose colonies seldom exceed 12 mm. in height (Billard gives 25 mm.); hydrocaulus monosiphonic, branching tends to be alternate and geniculate (Billard says quite irregular) with up to second order branching. Internodes usually somewhat curved, and irregularly wrinkled especially near their ends: sometimes part, or nearly the whole, of an internode may be smooth, the base being the narrowest part of the internode. Stolon formation from free ends quite common. Branches arise just below thecae, with a sharp turn upwards at the base of about 60° from their horizontal origin (assuming parent branch to be vertical); where two branches arise together, they do so in the same plane on opposite sides of the parent stem, usually with an axillary hydrotheca in between (fig. 13). Rarely, three branches may arise together in this way. As in other Haleciids new thecae grow directly out of the older ones, usually only one but in extreme instances up to three or

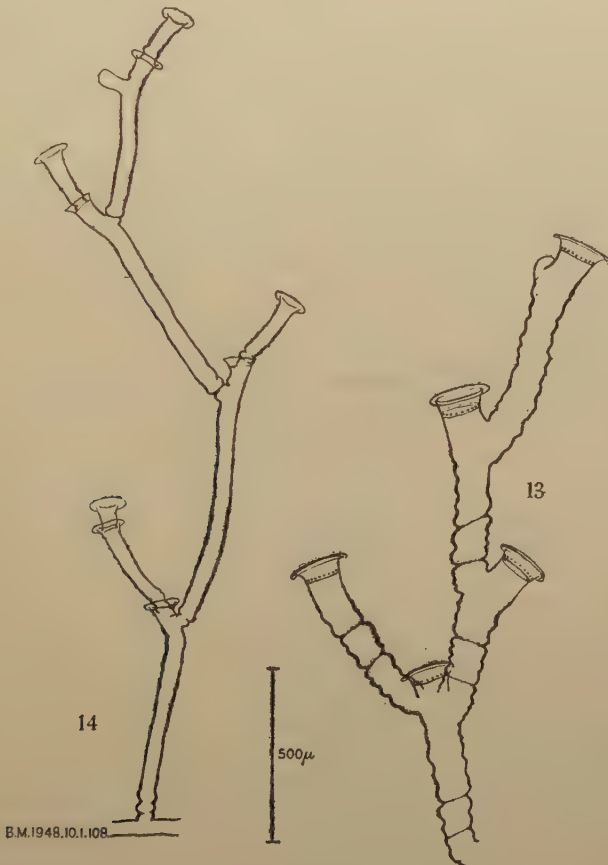


FIG. 13.—*H. undulatum*; a branch of the last specimen, more highly magnified to show details of perisarc, puncta and pseudodiaphragm.

FIG. 14.—*Halecium tenellum* Hincks. Portion of a colony, B.M. 1948.10.1.108, coll. E. T. Browne off Stoke Point near Plymouth, 3. xi. 1913, magnified to the same scale as fig. 13 for purposes of comparison.

four successively; in any case only the last, that with a polyp, has a pseudodiaphragm, though all thecae have puncta (Billard observed neither). This pseudodiaphragm is very thin and membranous, and slopes downwards at about 70° from the wall, extending inwards for nearly two-thirds of the radius of the theca at that level. The puncta are large and flattened, hence showing better in surface view than in optical section; in balsam mounts they are extremely difficult to see, but fresh and formalin material shows them very well. In the other thecae of the series, at pseudodiaphragm level, there is an annular shelf whose inner margin forms the base of the next theca rising up out of the one before. In rare instances, below the pseudodiaphragm, there is an annular thickening of the perisarc. The thecal rims expand funnel-wise and have their margins completely twisted over, more in the older than in the younger thecae. Polyp with a single whorl of up to 24, usually about 18 tentacles; the base of the polyp attaches peripherally to the puncta, and follows the slope of the pseudodiaphragm without actually resting upon it. Female gonothecae about the length of an internode, width more than half the length in one plane but only a quarter of it in the other plane (at right angles to the first); shape, smoothly and elliptically ovate, thin-walled and without any trace of ribs, spines or other ornamentation, distally somewhat pointed with an inconspicuous oval opening, proximally attached by a small tail-like footstalk arising within the theca or else from beside it; blastostyle surrounded by a central mass of developing embryos, but no hydranth pair.

Records.

On the keel of the West Hinder lightship, and inshore off the Dyck Bank, always on *Tubularia indivisa* (Billard, 1921).

53° 31' N., 01° 41' E., 4. v. 1950, fertile. Trawled on egg-capsules of	} Personal records.
<i>Buccinum undatum</i> ("Romilly").	
53° 05' N., 01° 10' E., 16. vi. 1951, loose in a whelk-pot (figs. 12, 13).	
53° 13' N., 01° 07' E., 27. v. 1954, on <i>Hyas araneus</i> .	

The following are in the British Museum of Natural History :

Trondhjem Fjord, coll. A. M. Norman, date unknown, growing on *Polynemertesia gracillima* (G. O. Sars).

Start Bay, Devon, coll. E. T. Browne, 28. vii. 1898, B.M. 1448.10.1.124.

Oban, Scotland, coll. A. M. Norman, 1877, B.M. 12.12.21.209.

Port Erin, I.O.M., coll. E. T. Browne, 16. viii. 1898, B.M. 1948.10.1.12.

Plymouth, coll. E. T. Browne, 1898, B.M. 1948.10.1.123, fertile (no date).

Loch Lorn, Scotland, coll. Sir John Murray.

Isle of Man, coll. J. Lomas. } No further details.

In the University Zoological Museum, Copenhagen, there were :

6 sea miles N. by W. of Store Kalsø, Faroe Islands, 60 fm., 25. v. 1899, fertile. Hvalfjord, Iceland, 46 m., 30. vi. 1904.

Stykkisholm, Iceland, 30 fm., 23. vi. 1897, fertile.

Seydisfjord, Iceland, 6 fm., 8. vi. 1900.

65° 02' N., 23° 56' W., 110 fm., 23. vi. 1896, fertile.

(These last five records are included by Broch (1918); the last one is his fig. XX on page 28, as *Halecium tenellum*.)

55° 12' N., 01° 25' W., coll. Ørsted.

55° 30' N., 01° 25' E., 20. vii. 1895, coll. Ørsted.

Vestmansund, Faroes, on *Delesseria*, 25 m., 24. ix. 1926.

60° 22' N., 47° 28' W., 120 m., 10. x. 1928, "Godthaab", stn. 188.

62° 08' N., 06° 31' W., 52 m., 24. viii. 1927, "Dana", stn. 3314.

Skagi, Iceland, 38 m., "Beskytteren".

62° 16' N., 05° 54' W., 94-113 m., 5. vii. 1902, "Michael Sars", stn. 44.

6 sea miles E. of Latrabjarg, Iceland, 22 fm.

Gullmarfjord, S. Sweden, 15. x. 1918 and 19. vii. 1929.

In the Skagerack, N.N.W. of Hanstholm, 70 m., 7. v. 1923, "Dana", stn. 3015.
59° 00' N., 03° 34' W., 66 m., 19. v. 1908, "Thor", stn. 2, fertile.

Most of these specimens in Copenhagen have been recorded (Broch, 1918; Kramp, 1929, 1932, 1938) as *Halecium tenellum*.

Halecium undulatum may thus be looked upon as a boreal species extending from the southern tip of Greenland, common at Iceland and the Faroes, to the North Sea, Norway, Skagerack, Belgium, West Scotland, Irish Sea, and the Channel. An interesting feature of the colonies listed above was that the wrinkling of the perisarc was most pronounced in Icelandic colonies, and decreased somewhat going south, so that a more straggling type of growth is often found in the southern North Sea: the two growth-types may be found in the same colony. Judging from Billard's figure, his types were of the slender form, while Broch's figure is of a fairly stout one (as are my own colonies, figs. 12, 13). Fertile colonies were found in the southern North Sea in early May, at the Faroes and the Orkneys in late May, and at Iceland in late June.

The true *Halecium tenellum* Hincks, of which the type is in the Natural History Museum, is only half the size all round of *H. undulatum*, and has perfectly smooth, very slender internodes, with widely everted thecae in piles of up to seven, and a general appearance of daintiness and fragility quite lacking in any other British species of *Halecium* (fig. 14). It is probably a more southern species than *H. undulatum*, but confusion among the small Haleciids is widespread, and great caution must be exercised in accepting any new records.

Lafoea dumosa (Fleming). Cast up in Blakeney Harbour, September 1949; taken at 53° 10' N., 01° 18' E., 17. vii. 1950; cast up at Hunstanton, 31. iii. 1953; cast up at W. Runton, 21. iii. 1954. The "Romilly" trawled many colonies in the open North Sea, where the species is more abundant than near the coast.

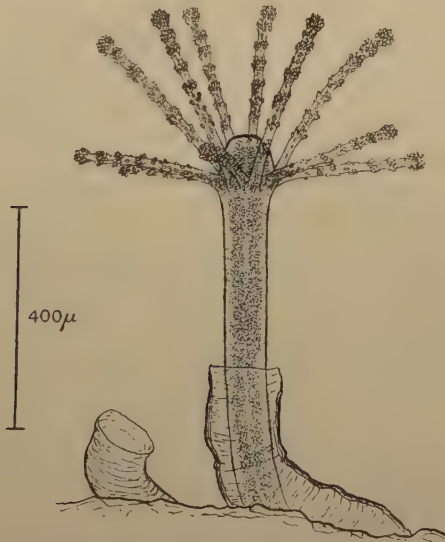


FIG. 15.—*Filellum serpens* (Hassall). Extended polyp, showing manner of holding tentacles. Cast ashore, Blakeney Harbour, July 1953.

Filellum serpens (Hassall). This is very common here on *A. abietina*, and less so on other large Sertularians. The coppinia forms a yellowish mat round the stem of the host, and the ova can clearly be seen among the accessory tubes which are straight or slightly curved; the breeding season here is from April to August. The polyp is shown in fig. 15, so far as I know for the first time; it has relatively few (about 12) tentacles, held alternately elevated and horizontally, with nematocysts tending to be clustered distally and scattered proximally, colour lemon-yellow when alive. There does not appear to be any diaphragm, or attachment puncta.

Cuspidella (? *costata* Hincks). A very small sterile hydroid cast up on *Flustra*, Weybourne, September 1949, is apparently this species or one like it. There is a certain amount of evidence (Russell, 1936, 1953) for linking *Cuspidella costata* Hincks with the medusa *Laodicea undulata* (Forbes & Goodsir) which occurs in the North Sea (Kramp, 1930) but not near here as yet.

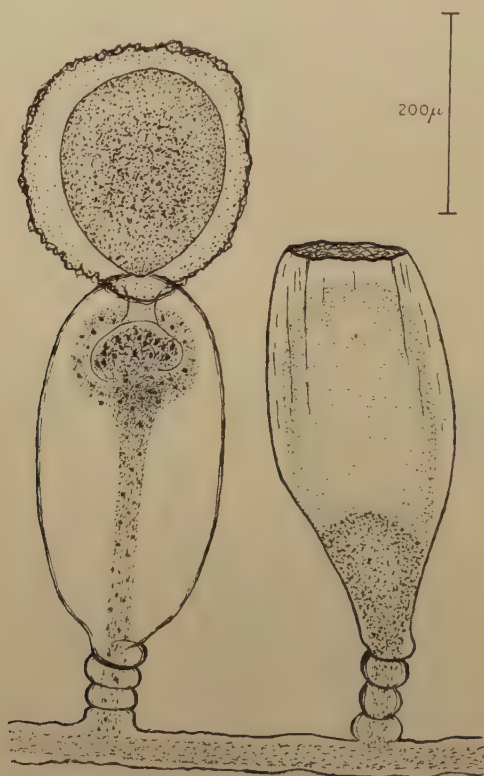


FIG. 16.—*Calyccella syringa* (L.). Gonothecae, female on left, male on right. In the female notice the inverted funnel-like tube of perisarc hanging down from the mouth of the gonotheca and enclosing the swollen apex of the blastostyle. On *Hydrallmania*, 53° 19' N., 00° 57' E., 22. vi. 1951.

Calyccella syringa (L.). Occurs abundantly on *Hydrallmania*, *Sertularia* and other large hydroids, especially if they are somewhat old. The length of the ringed hydrocaulus may be less than half that of the theca, or half as long again, but the other dimensions vary very little, and in any case are quite distinct from the next species. Gonophores of both sexes occur on the same stolon (fig. 16), one male to every six females approximately, so that it seems to be habitually hermaphrodite.

Fertile colonies were found by me south-west of the Dogger Bank in May ("Romilly") and in Norfolk waters in June, July, September and December.

Calycella hispida (Nutting). Syn.:

? *Lafoea pygmaea* Alder MS., in Hincks (1868), Northumberland.

Calycella pygmaea Thornely (1894). Isle of Man and Irish Sea.

Opercularella hispida Nutting (1898). Plymouth.

"? *Campanulina* ? spec." Hummelinck (1930). Nieuwediep, Holland.

My own records are:

On the wreck "Saint Guenowle" in Blakeney Harbour, Norfolk, at low water on *Scrupocellaria scruposa*, fertile 16. ix. 1951 (fig. 17); at Portchester, Hampshire, near half-tide level on *Bowerbankia imbricata*, fertile 5. x. 1951; and during December 1952 and January 1953, many sterile colonies on algae in creeks in the

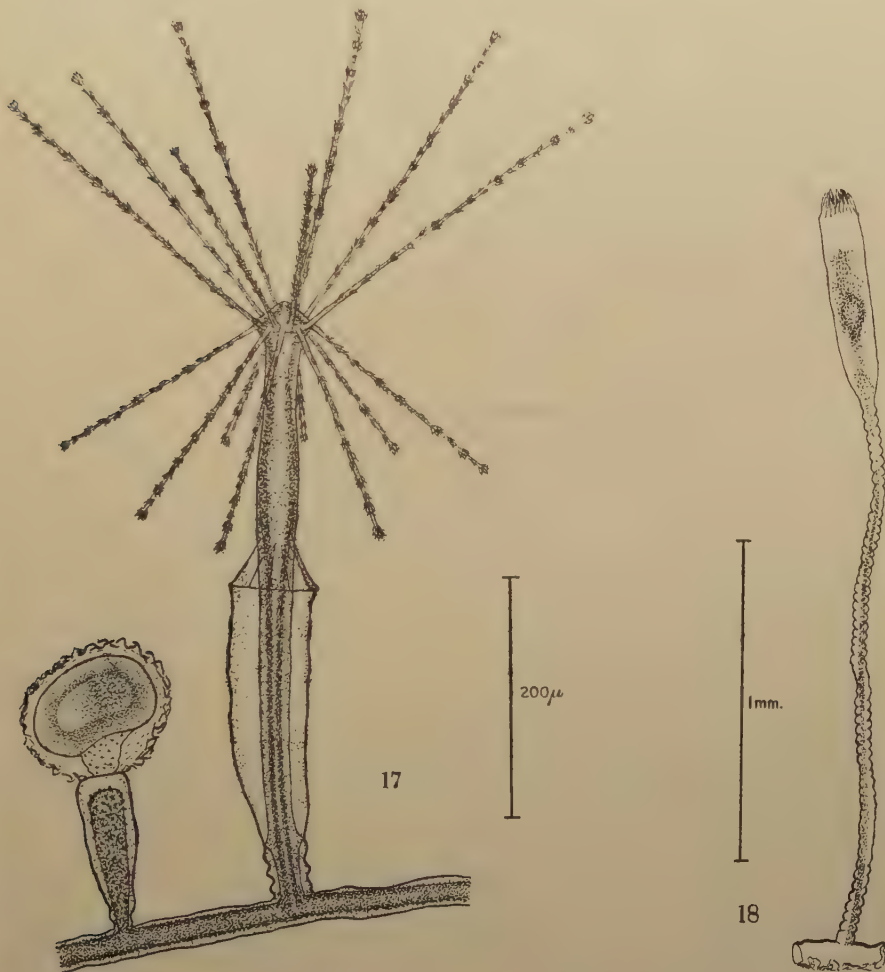


FIG. 17.—*Calycella hispida* (Nutting). On *Scrupocellaria scruposa*, "Saint Guenowle", Blakeney Harbour, 16. ix. 1951.

FIG. 18.—Calyccellid, gen. et sp. indet. Plankton, Blakeney Harbour, 20. iii. 1951.

marshes in Blakeney. Several points of interest were observed, and a description of the colony is as follows :

Polyps and gonophores arising singly at intervals from a thread-like stolon creeping over algae, polyzoa, and the like, in shallow water : hydrothecae rather slender and tubular, often slightly contorted, narrowing down to an indistinctly ringed or twisted base. Operculum composed of up to a dozen relatively stout segments with delicate folds in between, exactly as in *Calycella syringa* (Kramp, 1932, and own observations) ; no diaphragm, but a ring of attachment points just above the subspirally wrinkled lower portion (which is hardly distinct from the theca above). The living polyp when fully extended is twice as tall as the theca, with a conical hypostome surrounded by a single whorl of about 16 tentacles held alternately raised and depressed, the latter usually being shorter. The nematocysts of the tentacles tend to be single proximally and grouped in twos and threes distally, and have very long cnidocils. The external diameter of the polyp varies hardly at all, but in between the hypostome and the level of the operculum the coelenteron appears to expand internally, becoming narrower again below. (Living polyps of *C. syringa* had coelentera of uniform diameter, and were more than twice the size, with the thecal perisarc honey-coloured, dark yellow or dark brown : the perisarc of *C. hispida* is quite transparent, sometimes lemon-yellow, or amber-brown in the oldest thecae.) Gonothecae of *C. hispida* one-half or one-third as tall as the thecae : males not seen, females with a single ovum developing in an acrocyst, much as in *C. syringa*. Young unbranched colonies of *Opercularella lacerata* may be distinguished from *C. hispida* by their thecae being more oval and less tubular, with thinner walls, a larger, steeper and more delicate operculum of the Campanulinid, not the Calycellid, type (Kramp, 1932), and a more distinctly ringed thecal base. The expanded coelenteron is also present both in *Phialella quadrata* and *O. lacerata*, but extends right up to the inside of the hypostome, while that of *Calycella hispida* narrows off above its widest part, that is, below the tentacle-bases.

Calycellid, gen. et sp. indet. The fact that only isolated hydrothecae and hydrocauli have occurred means that a complete description is not possible, but a concise description is as follows :

A Calycellid with a filiform stolon, adhering to other substances, from which arise long simple spirally twisted hydrocauli, each bearing a theca at the upper end (fig. 18). Theca long and sub-cylindrical, narrowing off gradually into the stem below and widest at the rim. Operculum with about ten very delicate segments, of the Calycellid type (Kramp, 1932), height of closed operculum (height of apex above level of rim, measured along the axis of the theca) about two-thirds of the diameter of the rim. Polyp very extensible, with about 16 tentacles. In some polyps, but apparently not in all, the level where the theca joins the hydrocaulus is marked by a circle of attachment points (as in *Calycella hispida*). Total height (stolon to operculum) from 1.0 to 3.5 mm. In plankton from Blakeney Harbour, 30. vii. 1950 and 20. iii. 1951. Hartlaub (1897) described a very similar form as '*Calycella gracilis*' and suggested that it might be the hydroid of an *Aequorea* ; but the only species found here, *A. vitrina* (q.v.) has provisionally been linked with a very different hydroid, *Campanulina acuminata* (Alder) (see Russell, 1953).

Lovenella clausa (Lovén). Found only as dead hydrothecae in Blakeney Harbour plankton ; 28. vi. 1950 (one), 8 vii. 1950 (two), 20. iii. 1951 (two).

Phialella quadrata (Forbes). A large *Sertularia cupressina*, with a small Campanulinid smothering the branches up and down, was collected on the outside of Blakeney Point, cast ashore 26. viii. 1952. A few gonothecae were present (fig. 19), and after some days one liberated a young medusa which could be identified as *P. quadrata*. The fertile hydroid was also found on an old motor tyre below low-water in the Pit of Blakeney Harbour, 12. ix. 1950. The shoots are very appressed, all

the branches standing up together, while *O. lacerata* has its thecae standing out all round at about 60° to the vertical, and grows up to 10 mm. high (*P. quadrata* does not exceed 4 or 5 mm.). In young unbranched colonies the thecae of *quadrata* are more cylindrical and have a more distinct edge delimiting the operculum.



FIG. 19.—*Phialella quadrata* (Forbes). Colony cast up outside Blakeney Point, 26. vii. 1952. Although the coenosarc is poorly preserved, the gonotheca can be seen to contain a medusa-bud, the successor to that which was liberated and identified as *P. quadrata*.

Opercularella lacerata (Johnston). Small immature colonies can be seen in the Harbour at any time of year; on 27. iii. 1952, 18. ii. 1954 and 3. iv. 1953 large bushy colonies were obtained in Morston Creek with enormous acrocysts containing planulae, and with male gonothecae, both in great abundance. Opinions differ as to whether the small forms called *O. pumila* (Clarke) and *O. nana* (Hartlaub) are synonymous with *O. lacerata*; it appears, however, that the creeping habit and spindle-shaped gonothecae go together in *O. pumila* (see Hummelinck, 1936) and no such colonies have ever been seen here by me, although *O. nana* is recorded from Heligoland.

Campanularia volubilis (L.). This occurs commonly on the farthest whelk-grounds, about ten or twenty miles out, chiefly on *Hydrallmania* and *A. abietina*. It has a most distinctive habit of sending out a long tendril-like stolon which, on touching another branch of the host, immediately fixes on and twines around it, becoming festooned everywhere. The gonothecae are, according to Hincks (1868) "generally produced but sparingly", and once only have I obtained them, 16. vi. 1951, $53^\circ 05' N.$, $01^\circ 10' E.$, on *Hydrallmania*, amid many polyps. As a result, the frequency and abundance of the species become hard to explain unless (I venture this merely as an hypothesis) what are usually taken to be the swollen ends of tendrils are really masses of living material which then separate off and produce another colony by fixing elsewhere, a form of asexual reproduction. So far as I know this has never been seen in *C. volubilis*, but Hartlaub (1896) has observed it in *Stauridium productum* and Billard (1901) in *Laomedea geniculata*.

Campanularia integra MacGillivray. Colonies occurred on red algae low down the shore, at West Runton (fertile 15. ix. 1950) and more rarely in Blakeney Harbour. These specimens are much smaller than those I have seen from the Shetlands and from Iceland; and the shape of the theca, the amount of twisting of the hydrocaulus, and the thickness of the perisarc throughout, all seem to vary widely. It seems very sporadic in its occurrence; all mine were found in September 1950 and none since then.

Campanularia verticillata (L.). When trawling on the sandy grounds forty or fifty miles off the North Norfolk coast ("Romilly"), this species was obtained in quantities up to a small basketful per haul, but in local waters it is not at all common. For a large species it has surprisingly few epizoots ('lodgers') which normally infest the stouter kinds.

Clytia johnstoni (Alder). A very abundant, widespread form, on other hydroids, polyzoa, whelk-shells (rarely) and fragments of old timber; often very common in Blakeney Harbour on the red alga *Ceramium*. Gonothecae are found almost throughout the year, and the medusa (*Phialidium hemisphericum*) is, I should say, our commonest. The hydroid is very variable; the young thecae are narrow and deep, with few teeth, and have been described (Hincks, 1868) as '*Thaumantias inconspicua*' and '*Campanularia raridentata*'; Billard (1928) has linked them with *C. johnstoni*.

Genus *Laomedea* Lamouroux, 1812.

As understood here, this includes a large number of species whose trophosomes are all very similar but whose methods of reproduction vary widely. In shallow water along the Norfolk coast, in summer, these hydroids are the favourite food of the nudibranchs *Tergipes despectus* and *Eubranchius exiguus* which are very abundant and cover the colonies with masses of spawn.

Laomedea (*Obelia*) *geniculata* (L.). In coastal waters around other parts of the British Isles where *Laminaria saccharina* is abundant, *L. geniculata* grows thickly upon it, but on this coast *L. saccharina* is rather scarce, and most of my records are on *Flustra foliacea*, floating corks, and larger hydroids, rarely on stones and shells.

Laomedea (*Obelia*) *longissima* (Pallas). This species is often approached very closely by the next, but has a very distinct black main stem and hydrothecae of circular section with toothed rims, nor does it ever occur on the shore save when cast up. It seems to grow mainly on shells and stones rather than on other hydroids, rarely on polyzoa.

Laomedea (*Obelia*) *dichotoma* (L.). Two intergrading forms of this species can be distinguished in Norfolk waters:

- (i) The typical *L. dichotoma*, up to 40 mm. high, found only offshore and often cast ashore epizootic on larger forms. The polyhedral thecae have almost even rims.
- (ii) A large form (*Obelia flabellata* Hincks) which occurs in thick tufts all over the mussel-lays in summer (cf. Dales, 1951) and whose thecal margins are more sinuated than in the offshore form, sometimes approaching teeth. The method of branching of the colony is less 'open' than in true *longissima* (which it otherwise closely resembles) and is only an overgrown version of the typical growth-form.

Laomedea (*Obelia*) *bicuspidata* (Clarke). This may be called a circumtropical species; the British Isles, for which this is the first record, lie very much at the northern limit of its distribution. It was first described from Long Island (Clarke, 1875) and since then has been found many times. Details of synonymy are set forth in Stechow (1912, 1919) and in Hummelinck (1936). In British waters I have

found it rather commonly along the Norfolk coast: at Hunstanton it seems to be abundant close offshore as many colonies are cast up, one of which, on 27. ix. 1953, was nearly 35 cm. high. Only once have I seen it from far out to sea, at $53^{\circ} 15' \text{ N.}$, $02^{\circ} 45' \text{ E.}$, one small colony collected by the Ministry of Fisheries vessel "Sir Lancelot". In Blakeney Harbour it has occurred growing in the creeks and at the far end of the Harbour below low-water; while along the whole north Norfolk coast small colonies are found washed ashore attached to other hydroids and to branching polyzoa. I have never taken it on the whelk-grounds. At Hunstanton, 5. ix. 1952, on "Saint Guenowle", 16. ix. 1951, and at West Runton, 1. viii. 1954, I found fertile colonies, the last-mentioned releasing typical small '*Obelia*'-medusae,

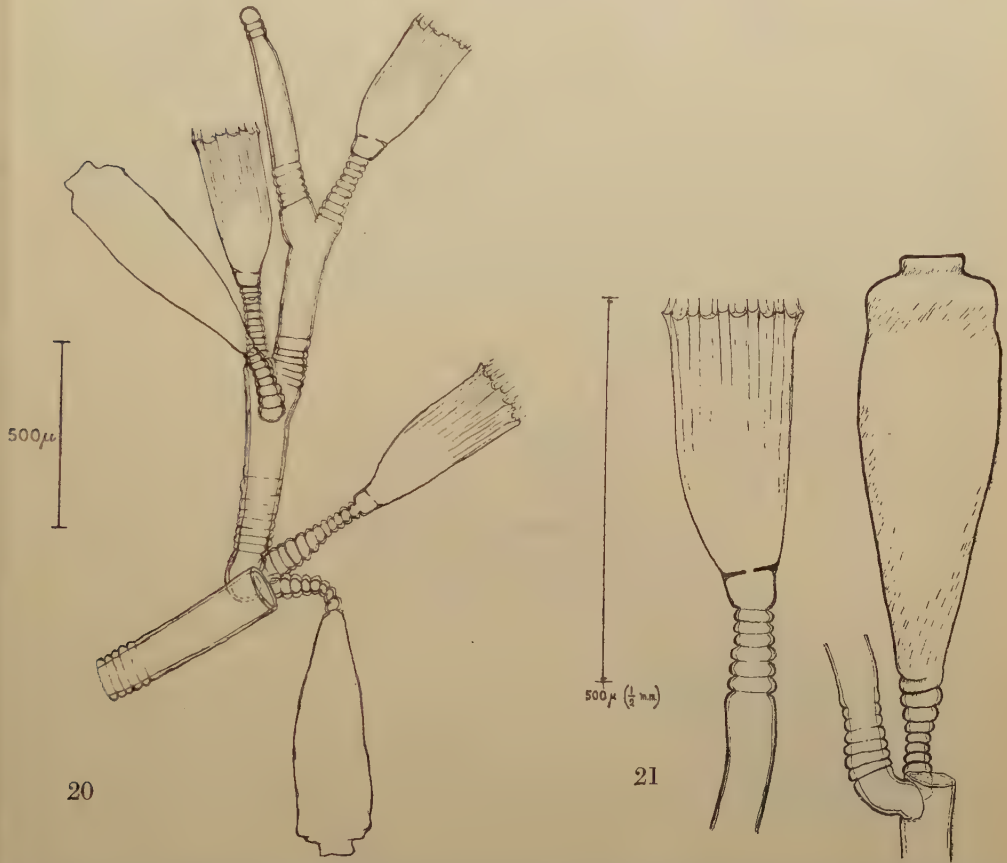


FIG. 20.—*Laomedea bicuspidata* (Clarke). Part of a colony cast up at Hunstanton, 5. ix. 1952.
FIG. 21.—*L. bicuspidata*. Hydrotheca and gonotheca more highly magnified, from the last-named.

exactly like those of *L. geniculata* or *L. dichotoma*. It greatly resembles *L. gelatinosa* in its mode of growth, but the chief difference is in the hydrothecae; those of *bicuspidata* are very long and deep, slightly asymmetrical, with numerous carinae in the radial plane running up the inside of the theca and coming to a sharp triangular point above the rim, which undulates between them, alternately high and low, so as to give a paired effect to the spinulose points of the carinae (figs. 20, 21). All the other Campanularian hydroids in European waters have thecae whose rims, if toothed, are cut into a simple battlemented or cusped pattern.

Laomedea (Obelaria) gelatinosa (Pallas). Not found very often, probably because it lives a little way outside Blakeney Point where no fishing is done that would catch it. It has a habit of occurring in vast amounts, thick bushy colonies up to 22 cm. high from a matted rooting system, cast up in every pool and creek, and then of being quite unobtainable for some months.

Laomedea (Gonothyræa) lovéni Allman. This is the commonest hydroid in Blakeney Harbour, especially in the creeks, on stones and *Fucus*. Its curious reproduction (in spring and summer) has attracted the attention of many authors and, although it suffers from being heavily grazed by pycnogons and nudibranchs of several species, it still maintains its abundance. Once I fed a minute polychaete to a hungry *L. lovéni*; the tentacles slowly curled round it while the hypostome flapped violently in and out, almost as if the polyp was smacking its lips! The head end of the worm was too large to go in, so with much fumbling a reversal was effected in just under 17 minutes. At this point the experiment was broken off. Rarely, such interesting anomalies as branched tentacles may be seen, while the perisarc is often smothered with vorticellids and minute algae.

Laomedea (Gonothyræa) hyalina (Hincks). Abundant off the Norfolk coast on larger hydroids, also on *Hyas araneus* and *H. coarctatus*. Nutting (1898), alone of modern authors, believes that this and the last intergrade. My own experience is that *hyalina* has a distinct and bare main stem below, and several branches all coming off together. The separate joints and branchlets are very delicate and all arise nearly vertically, so that a rather trim and delicate tuft results, in contrast

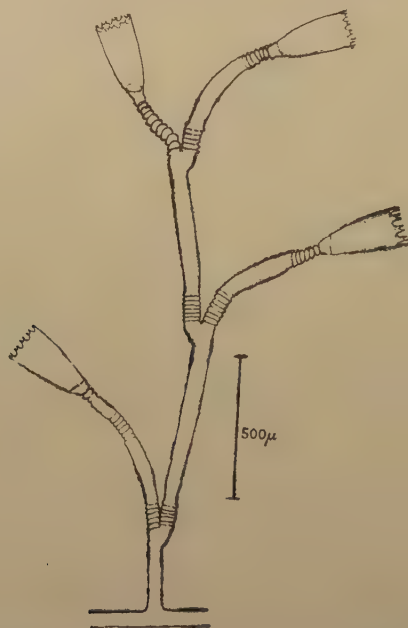


FIG. 22.—*Laomedea neglecta* (Alder). Showing branching and bicuspid teeth.

to the robust and straggling growth of *L. lovéni*, which also has smaller thecae without lines running down the sides from the (smaller) marginal teeth. *L. hyalina* occurs only out to sea and is a more northern species than the littoral *L. lovéni* (Kramp, 1911, 1929, 1932, 1938). As Hincks surmised, the method of reproduction is the same in both; in these waters *L. hyalina* breeds from April to September, and *L. lovéni* from March to August, the maxima being summer and spring respectively.

This is probably the farthest south in the British Isles where *L. hyalina* is at all common.

Laomedea (Gonothyraca) neglecta Alder. This species is very liable to be confused with young *L. loréni*, and may be more common than the records would seem to indicate: they are: on a stone in the meshes of a whelk-pot, 53° 15' N., 01° 02' E., 2. vii. 1952, sterile (fig. 22), and among *Bowerbankia imbricata* under rocks near Wells Quay, 18. ix. 1954, fertile. See also Hincks (1868, 1872) and Hummelinck (1930, 1936).

Laomedea (Campalaria) conferta (Hartlaub). On 22. vi. 1951, at 53° 19' N., 00° 57' E., fertile colonies were found growing on *Hyas araneus*, corresponding exactly to Hartlaub's account (1897). The diaphragm in the hydrotheca is always tilted towards the axis of the main stem, that is to the 'right' in the thecae coming out on the 'left'-hand side (fig. 23.) Fine large sterile colonies have since been taken on the ascidian *Styela coriacea* off Sheringham, 53° 30' N., 01° 10' E., 2. vii. 1951; and at 53° 05' N., 01° 10' E., 16. vi. 1951 (re-examined after finding the others). The late Sir Sidney Harmer found a hydroid at Yarmouth in 1899 (quoted by Garstang, 1900) on *Sabellaria* tubes near the shore, as were Hartlaub's type specimens. Harmer referred his colonies to *Laomedea exigua* M. Sars, whose thecae are very like those of *conferta*.

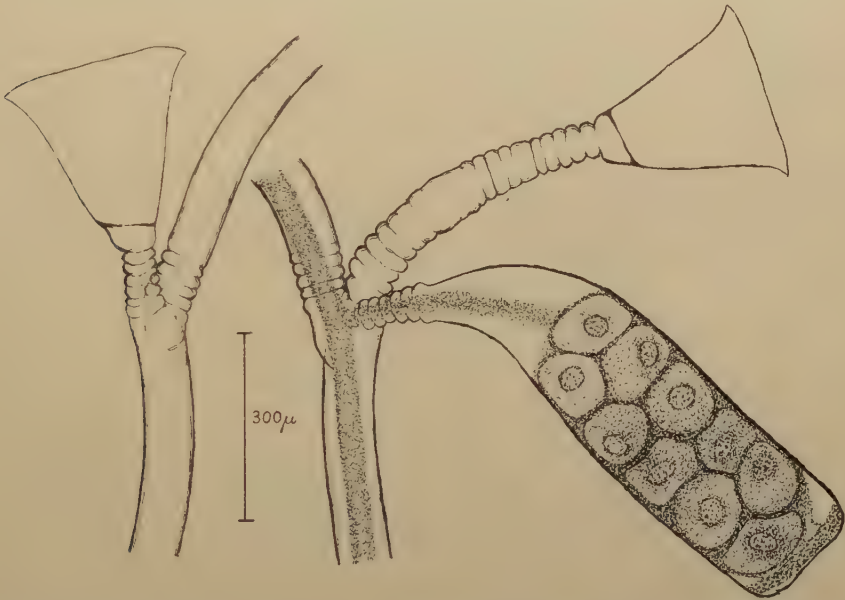


FIG. 23.—*Laomedea conferta* (Hartlaub). Left, a hydrotheca with tilted diaphragm and short pedicel; right, a similar theca with long pedicel, and a gonotheca packed with ripe ova. Off the Race Bank, 53° 19' N., 00° 57' E., 22. vi. 1951.

Laomedea flexuosa Hincks. Found in the lower part of Blakeney Harbour in fair quantities on *Fucus vesiculosus*, but not common in creeks; less abundant than *L. loréni* and does not extend so far up the shore.

Sertularella rugosa (Gray). Has a practically exclusive preference for the polyzoan *Flustra foliacea*, but is not very common here though in south Kent (Dungeness) every colony of *Flustra* was covered with it. Specimens trawled near the Dogger Bank ("Romilly") were much larger than those taken just offshore in whelk-pots.

Sertularella polyzonias (L.). This is a common species in other waters, of which I have few records here, possibly because it does not live near any whelk-grounds ; an extensive dredge and trawl survey would no doubt yield much more, as in several other species.

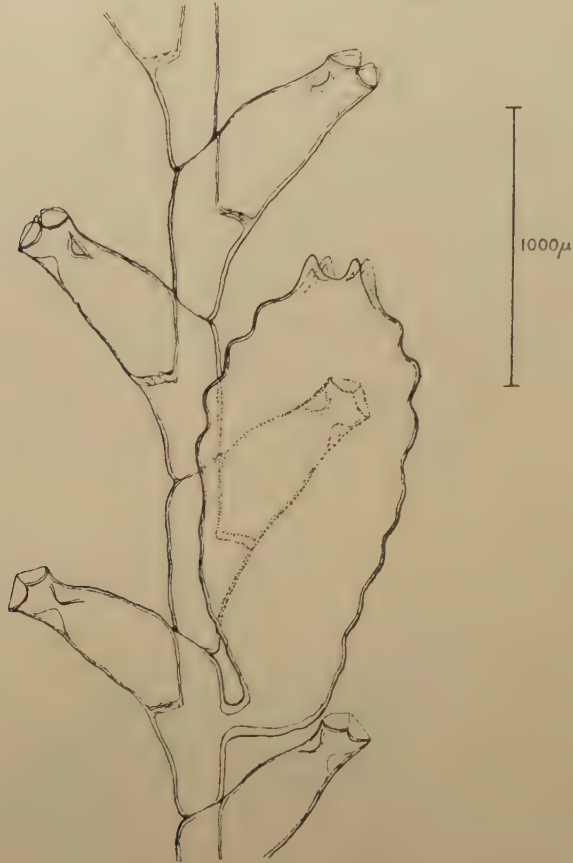


FIG. 24.—*Sertularella mediterranea* Hartlaub. Hydrothecae and gonotheca.
"Iron Steamship", Blakeney Harbour, 10. vi. 1952.

Sertularella mediterranea Hartlaub. This species is very closely related to the last, and it has been a matter of dispute whether they are varieties or distinct species. I have never seen any intermediates but, according to Stechow (1919), these are common in the Mediterranean. The chief difference, in all the specimens I have seen myself, is in the hydrothecae, which in *mediterranea* are produced and rather spout-like with a small 4-leaved operculum and, just inside the mouth, three teeth projecting inwards from the sides ; one abcauline in the plane of the theca and hydrocaulus, and the other two at 120° to the first. I have also seen this form at Skokholm in South Wales (personal coll.), in the Solent (B.M. 86.10.4.4) and the Hebrides (Canon Norman coll., B.M. 12.12.21.139a) ; while the literature records it from the Channel Islands (Verwoort, 1949), the Breton coast (Bedot, 1911, 1914 ; Billard, 1912) and in many places farther south (Stechow, 1919). The thecae in typical *polyzonias* are shorter, just as if the spout-like portion with internal teeth was cut off and a new and larger 4-valved operculum fitted over the opening. The

gonothecae appear to be identical in both ; to the naked eye, colonies of *mediterranea* are noticeably more delicately built. My Norfolk records are as follows :

"Iron Steamship", L.W.S.T., 10. vi. 1952, fertile (fig. 24).

Hunstanton, cast up 27. ix. 1953, fertile.

West Runton, growing under rocks, 1. viii. 1954, sterile.

West Runton, cast up 16. ix. 1954, fertile.

"Iron Steamship", L.W.S.T., 21. vi. 1955, fertile and unusually abundant.

"Iron Steamship", L.W.S.T., 23. vii. 1955, fertile.

53° 09' N., 00° 53' E., dredged 20. ix. 1955, fertile, on shells and *Sabellaria*.

Whereas in 1949 and 1950 several large colonies of *polyzonias* were cast ashore, since then few have been seen, and all of them small, while *mediterranea* appears to be increasing.

Abietinaria abietina (L.). A very common species, usually infested with epizoots such as *Filellum*, *Electra pilosa*, *Crisia aculeata* and *C. eburnea*, *Spirorbis spirillum*, and foraminifera. One of the few Norfolk hydroids noticed by Sir Thomas Browne (1600-1680) who called it a '*Fucus*'; he found it near Hazeboro'. It prefers a sandy bottom with small stones and shells, and is a winter and spring breeder.

Abietinaria filicula (Ellis & Solander). The only records are of a dead colony in Blakeney Harbour, September 1947, and of one dead and one living but sterile at Hunstanton, 23. iii. 1952.

Hydrallmania falcata (L.). This is one of the commonest hydroids on the offshore grounds, sometimes attaining a height of 20 cm., and in old colonies often encrusted with ascidians such as *Botrylloides*, polyzoa (mainly *Electra pilosa*), and small hydroids, especially *Calycella syringa* and *Halcium beani*.

Diphasia rosacea (L.). Although this species is common here I have never found specimens exceeding 3 cm. in height in Norfolk waters, whereas this was almost the minimum size of magnificent specimens trawled in great abundance on the Dogger Bank and to the south-west of it in May 1950, by myself on the "Romilly".

Diphasia attenuata Hincks. Occurs fairly commonly, but in nothing like such abundance as *rosacea*, with which it is sometimes associated.

Dynamena pumila (L.). In many parts of the country this is a very common species on *Fucus*, but in Norfolk I have only seen it at West Runton, under large stones and boulders at low water of neap tides and below, and very rarely creeping out across a frond of *Fucus*. It is heavily grazed by *Facelina longicornis*, the commonest and one of the most beautiful of the nudibranchs found there, and is often overgrown with small algae, protozoans and *Pedicellina cernua*: I have never seen it from out to sea, where the next species is usually found.

Sertularia gracilis Hassall. From time to time there has been a sharp divergence of opinion as to whether this and *S. distans* Lamouroux are distinct species; Picard (1952) says that *distans* has the axial part of the thecate portions of the stem much thinner, the neck of the gonotheca much wider and shorter, and that the ectoderm of the polyp in *gracilis* is covered with small dark speckles which *distans* apparently lacks (but which I have seen in living colonies of *gracilis* taken at Hunstanton). The perisarc agrees in Norfolk waters with the excellent figure given by Billard (1925). This hydroid is almost always found upon old dead *Hydrallmania* stems; fertile colonies have been found in July.

Sertularia cupressina (L.). A very abundant hydroid here, heavily browsed-over by the nudibranch *Doto coronata* and by pycnogonids. When growing in shallow water it is often covered with small algae, hydroids, polyzoa and protozoa, so as to disguise it most effectively.

Amphisbetia operculata (L.). The stems of this hydroid are a favourite abode of small polyzoa (*Cellepora avicularis*, *Hippothoa hyalina*) and foraminifera. It is locally a characteristic form of the Laminarian zone and breeds in summer.

Thujaria thuja (L.). The only Norfolk colonies recorded are a small stem with three or four branches in Morston Creek, cast up 1. i. 1950; another tuft at Hunstanton 28. xi. 1950, and one on Cley beach, 8. iii. 1950. Garstang (1905) stated that "So great is the disturbance of the sea bottom during these winter gales on the shallower central grounds such as the Dogger and Well Banks, that the Hydroid Zoophytes, which are so abundant in these localities, are rolled by wave action into compact fibrous balls from four to eight inches in diameter". The specimen of *T. thuja* from Morston Creek was right in the middle of just such a surf-ball, composed mainly of *Hydrallmania*, together with *Eudendrium rameum*, *E. ramosum*, *Bougainvillia ramosa*, *Tubularia indivisa*, *Clytia johnstoni*, *Laomedea longissima*, *L. dichotoma*, *L. gelatinosa*, *Campanularia verticillata*, *Calycella syringa*, *Lafaea dumosa*, *Halecium halecinum*, *H. beani*, *Sertularella polyzonias*, *Diphasia rosacea*, *D. attenuata*, *Sertularia gracilis*, *Abietinaria abietina*, *Sertularia cupressina*, *Nemertesia antennina*, *N. ramosa* and *Kirchenpaueria pinnata*: a total of twenty-four species in a mass of hydroids about 20 cm. in diameter; such abundance is seldom met with.

Kirchenpaueria pinnata (L.). The offshore form corresponds exactly to *pinnata* and the littoral form to *echinulata* as described in Hincks (1868), but the variations of the shore form intergrade with those of the offshore form in such a way as to indicate that only a single species is involved. The littoral variety grows in thick tufts on *Mytilus*, on *Fucus* and *Chorda filum*, rarely upon *Laminaria* stipes, and the other on sponges (cf. Wilson (1947), plate 7; I had beautiful colonies on a sponge from 53° 10' N., 01° 10' E., 2. vii. 1951, (fertile) or implanted as a form of camouflage on the carapace of *Hyas araneus* (see remarks on *Nemertesia*, below). Such specimens often show regeneration of the hydrorhiza and appear as healthy as if in their original habitat, though they are usually too small to be fertile.

In September 1950 the nudibranchs *Galvina vittata* and *G. cingulata* were found in small numbers feeding on it and spawning on the branches, around the mussel-lays in Blakeney where the var. *echinulata* is very abundant.

Plumularia setacea (Ellis & Solander). Not very common, perhaps because of the lack of shelter. At Weybourne, 12. vii. 1949; a large colony on *Mytilus*, Blakeney Harbour 24. ix. 1949; on whelk-grounds, 53° 11' N., 00° 57' E., 1. viii. 1950 and 53° 05' N., 01° 10' E., 2. vii. 1951; and always abundant in "Saint Guenowle" and the "Iron Steamship" where it is sheltered under ideal conditions, during the entire breeding season from June to September.

Plumularia allenii Nutting. This is the only hydroid added to the Norfolk fauna during a whole summer's dredging, May to September 1955; an indication that few species remain undetected locally. Many fertile colonies were found on *Nemertesia ramosa*, chiefly near the apices of the main shoots; this agrees with my experience of material from Plymouth, where *P. allenii* is common on *N. ramosa*, but very rare on *N. antennina*. *Plumularia setacea* will, however, grow near the base of *N. antennina*; such colonies were found, with the *allenii* on *N. ramosa*, at 53° 09' N., 00° 53' E., on 20. ix. 1955, in the last dredge haul of the season.

Plumularia halecioides Alder. Only under rocks near low-water mark at West Runton, 15. vii. 1950, 4 and 6. ix. 1952, 4. x. 1952, 26. viii. 1953, none fertile.

Plumularia diaphana (Heller, 1868) syn. *P. cornucopiae* Hincks, *P. alternata* Nutting. At West Runton with the last species, 4 and 6. ix. 1952, sterile. So far as I know this is the first North Sea record and the farthest north that the species

has ever been found. It appears to be an immigrant from the tropics, where it enjoys a world-wide distribution (cf. *Laomedea bicuspidata*). Previously in this country it was found at Ilfracombe in Devon (types of *P. cornucopiae* Hincks, 1872) and at Plymouth (1931). Stechow (1912) gives a description and figure of specimens from Villefranche (south coast of France) which, he avers, are undoubtedly identical with Heller's original specimens, and which are exactly like Hincks's Ilfracombe drawings and my own specimens from Runtou (fig. 25). Stechow (1919) gives many records with synonymy. In British waters it may be confused with *Halopteris catharina* (see Hincks, 1868, as *Plumularia*; also Totton, 1930), but in the latter

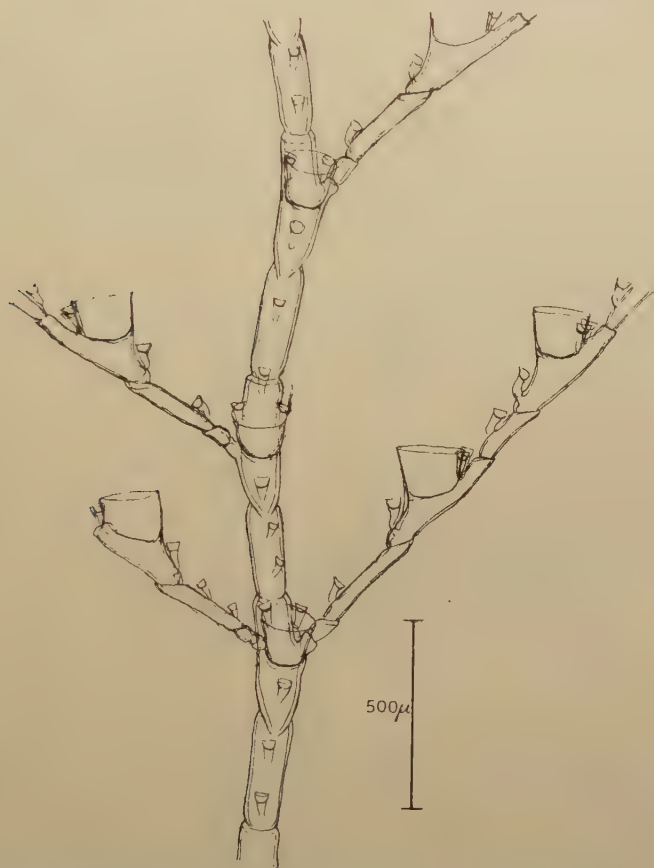


FIG. 25.—*Plumularia diaphana* (Heller). Lower middle part of a single tuft; lower left, a short hydroclade arising abnormally opposite a normal hydroclade. West Runtou, 4 and 6. ix. 1952.

the branches arise alternately, while *diaphana* has them in opposite pairs (though both species occasionally vary in this respect); in *catharina* there are two pairs of nematophores flanking the hydrotheca, in *diaphana* only one: finally *diaphana* is much slenderer and smaller overall (Ritchie, 1913 a; and my own observations). So far *catharina* has not been recorded from Norfolk waters, but it may well occur here, as it is fairly common off Northumberland and in the Channel.

Nemertesia antennina (L.). A common hydroid off the Norfolk coast, and widely distributed in the North Sea. In the summer of 1949 enormous amounts were cast ashore at Weybourne, so that the beach was heaped with it. The spider-crabs

Hyas araneus and *Hyas coarctatus* (which infest the crab- and whelk-pots) are often found with small colonies epizoic on them, and examination shows that they have not arisen by the settling of a planula on the crab's carapace, but that they are in fact the apical 3 cm. or so of a large tuft growing on the sea-bottom in the normal way, which the crab has ascended to pinch off the end portion required. The selected piece is filled with active coenosare, and on being planted on the crab's back sends forth small rooting processes; in large mature colonies the stem is dead nearest the hydrorhiza, while in these 'cuttings' it is alive. Occasionally in such a 'cutting' a new stem with branches grows out of the base of the first stem, and in the opposite direction; such bipolar colonies may be produced both by *N. ramosa* and by *N. antennina* when rooted on a *Hyas*.

Nemertesia ramosa (Lamouroux). This species is much less abundant here than is *antennina*. Although I was familiar with it, having seen it at Plymouth and in Kent, I never found any until late November and December 1949. Within a few weeks large colonies were being washed up in numbers every day in Blakeney Harbour, on the outside of the Point, and at Hunstanton. Weybourne and West Runton had rather fewer colonies than elsewhere. By the end of January 1950 there was comparatively little left, since when it has survived in small quantities.

2. (b).

(i) PREVIOUS RECORDS OF NORFOLK HYDROIDS, NOT SEEN PERSONALLY.

Hydranthea margarica Hincks. Taken at Yarmouth in 1899 by Sir Sidney Harmer, growing on *Flustra foliacea* (Garstang, 1900) from which Hincks also took his specimens. The *Plymouth Marine Fauna* (1931) records it on broken whelk-shells and on a stone.

Laomedea exigua M. Sars. I have already dealt with this under *L. conferta*; but of course it is perfectly possible that the true *L. exigua* is a distinct species which also occurs here, though I have never seen any specimens which I could refer to it.

Sertularella gayi (Lamouroux). Reported off here by Peach (*vide* Hincks, 1868) but I have a shrewd suspicion that he was dealing with large *polyzonias*.

Thuiaria articulata (Pallas). Recorded locally by Peach; a characteristic form which seems to be scarce in the North Sea.

(ii) SPECIES, FOUND IN NEIGHBOURING WATERS, WHICH MAY OCCUR OFF THE NORFOLK COAST.

Zanclaea implexa (Alder). I have collected the hydroid with many ripe medusa-buds at 54° 08' N., 00° 40' E., on 1. v. 1950, growing all over a dead valve of *Cyprina islandica* ("Romilly").

Halecium labrosum Alder. A northern form (Broch, 1918; Kramp, 1929, 1932, 1938) known from Northumberland, the east of Scotland (Hincks, 1868) and from the open North Sea (57° 40' N., 02° 30' E., 37 fm. and 55° 30' N., 01° 00' E., 40 fm., personal observations). A fragment was also taken at Plymouth (1931).

Sertularella tenella (Alder). Very abundant on the Dogger Bank in May 1950 ("Romilly") and may possibly occur in these waters.

(iii) THE NORFOLK MEDUSAE.

In every case except where otherwise stated the medusae were captured in a plankton net towed behind a small boat for about 45 minutes just below the surface, in Blakeney Harbour.

Sarsia eximia (Allman). See above, under *Coryne eximia*; never taken here in plankton.

Sarsia tubulosa (M. Sars). See above, under *Coryne tubulosa*.

Rathkea octopunctata (M. Sars).

20. iii. 1951. Three, all with buds.

17. iii. 1954. Two, one with buds.

7. iv. 1954. One, with buds.

8. iv. 1954. One, with buds.

19. iv. 1954. Seven, some with buds.

22. iv. 1954. 130 to 140, including every stage from very small medusae to full-sized individuals carrying buds as large as the youngest medusae present.

Bougainvillia ramosa (van Beneden). See above, under hydroid ; also one young one, 20. iii. 1951.

Leuckartiara octona (Fleming). 9. iv. 1952, one very young one.

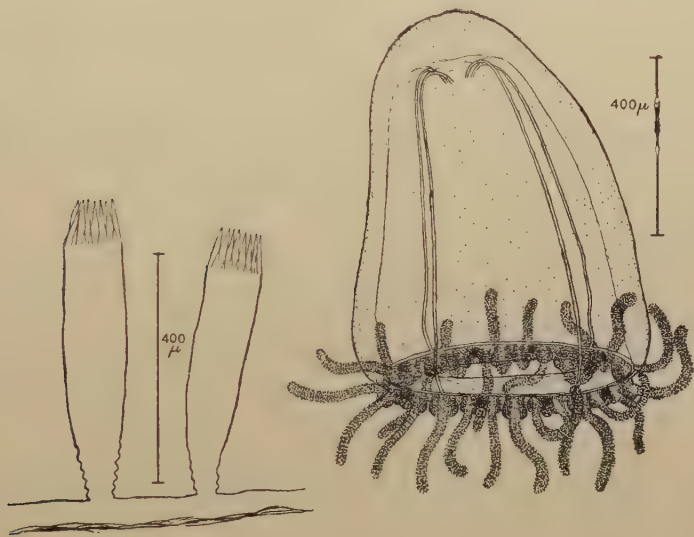


FIG. 26.—*Tiaropsis multicirrata* (M. Sars). Hydroid from off Northumberland, medusa from Blakeney Harbour. The manubrium had been lost, probably because of injury.

Staurophora mertensi (Brandt). The identification was kindly confirmed by Mr. F. S. Russell. The records are :

5. iv. 1954. One young one ; and two days later thirteen more, ranging from 0.75 mm. to 2.00 mm. in height of bell. None showed any sign of maturity. All were unfortunately destroyed in the post.

22. iv. 1954. Two, det. F.S.R., of the same size as the others.

Tiaropsis multicirrata (M. Sars).

20. iii. 1951. One (fig. 26).

7. iv. 1954. One, same size.

The hydroid shown in fig. 26 is from 55° 12' N., 01° 24' W., coll. Ørsted, 1910, and agrees with that described by Rees (1941) from the Clyde. I am grateful to Dr. W. J. Rees for confirming the identity of this hydroid.

Obelia spp. and *Phialidium hemisphaericum* (L.). These medusae are so common that detailed records are unnecessary; they are found all the year round but are very scarce from November to March, and are most abundant in June, July and August.

Phialella quadrata (Forbes). See under hydroid; never taken in plankton.

Aequorea vitrina Gosse. Occurs every year in June and July, up to about 150 mm. in diameter and often in great abundance. On calm sunny days they swim gently just below the surface, often breaking it, and showing a violet fluorescence as though lit from within.

Eutima gracilis (Forbes & Goodsir). 17. ix. 1953, one, 10 mm. diameter, and two days later another one, 6 mm. diameter.

Tima bairdi (Johnston). On 11. iii. 1955 I found six large mature specimens of this medusa, left by the ebb-tide in Morston Creek, and still alive. They were possibly members of a shoal blown here by a bitter north-east wind which at that date had been blowing for some weeks.

2. (c) ZOOGEOGRAPHICAL RELATIONS OF THE NORFOLK HYDROIDS.

The various species will be taken in groups according to their distribution elsewhere.

- (a) Species with a northern and Arctic distribution: *Halecium muricatum*, *Campanularia volubilis*, *Laomedea hyalina*, *Thuiaria thuja*.
- (b) Species with a southern and Mediterranean distribution: *Halecium lankesteri*, *Laomedea bicuspidata*, *Sertularella mediterranea*, *Plumularia diaphana*.
- (c) Boreal species, found all around the British Isles and ranging slightly north and/or south; these include all other species on the list, except for:—
- (d) Species with an insufficiently known range: *Clavid* sp. indet., *Trichydra pudica*, *Halecium undulatum*, *Calycella hispida*, *Lovenella clausa*, *Calycellid* sp. indet., *Laomedea conferta*.

While all the hydroids in (a) are common forms in the open North Sea, those in (b) are either unknown or else (*L. bicuspidata*) very scarce there, appearing to be commonest near the coast. All the (a) species may be cast ashore from time to time, but none lives nearer land than about a mile.

The period of the breeding season does not appear to bear any direct relation to the geographical range of the species concerned; it can, however, be shown that species breeding most of the year (e.g. *Clytia johnstoni*, *Sertularia cupressina*) although possibly not more abundant than those which confine their activities to an intensive season of a few weeks (e.g. *Eudendrium arbusculum*, *Laomedea loveni*, *Clava multicornis*, *K. pinnata*), are more evenly distributed throughout the year; in other words, the second group flourish for a while and during the rest of the year are scarce or absent.

These breeding records refer only to sexual reproduction, entailing the production of medusae or sporosacs. Such phenomena as the formation of stolons or 'frustules' (e.g. Kramp, 1911) have not been systematically recorded; but from my observations here I should say that almost any species will form them, mostly under rather unfavourable conditions.

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THE LINNAEAN SPECIES OF CARABID BEETLES. By CARL H. LINDROTH,
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Zoological Secretary.)

(With 1 text-figure.)

[Read 19 January 1956.]

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INTRODUCTION.

Almost all the Carabidae (incl. Cicindelinae) described by Linné under binomial names were placed by him in his genera *Carabus* and *Cicindela*, the number of species being altogether 45 within the former, 14 within the latter genus. As demonstrated below, however, two (or even three) of the 'Carabi' are foreign elements, belonging to other beetle families. On the other hand, three species placed by Linné in *Attelabus* and three in *Tenebrio* are true Carabids, though of the last-named two are conspecific. The total number of Carabid species described by Linné thus amounts to 61 (or 62).

An interpretation of the Linnaean species names can be based on three groups of facts:

(1) *Linné's own descriptions*. As far as Carabids are concerned, these may be found in the following works:

(1736.) *Animalia per Sueciam observata. Acta Literaria et Scientiarum Sueciae.*
4. Uppsala.

(1746.) *Fauna Suecica*. Ed. 1. Stockholm.

(These two works are without binomial names.)

1758. *Systema Naturae*. Ed. 10. Stockholm.

(First application of binomial nomenclature.)

1761. *Fauna Suecica*. Ed. 2. Stockholm.

1763. *Centuria Insectorum Rariorum*. (Resp. Boas Johansson.) *Amoenitates Academicæ*. 6. Uppsala.

1764. *Museum Ludovicæ Ulricæ*. Stockholm.

1767. *Systema Naturae*. Ed. 12. 1 (2). Stockholm.

1771. *Mantissa Plantarum*. Stockholm.

These are cited below under the year of publication alone.

(2) *Linné's original specimens*, often regarded as 'types'. The main collection belongs to The Linnean Society of London (*vide* Jackson, 1913); a small number, mainly of species described in 1764 (earlier in the Drottningholm Museum, Stockholm), are in the Zoological Institute of the University, Uppsala. One or possibly two Linnaean 'types' could also be discovered in the collections of the Swedish Riksmuseum, Stockholm.

(3) *The practice of using Linnaean names* applied by his contemporaries and early successors, within entomology especially by J. Chr. Fabricius (1745-1808). It seems, however, that the opinions of Fabricius and others were based on the Linnaean descriptions alone.* Linné apparently, during his lifetime, never dispersed his specimens among other scientists and collectors (*vide* Löwegren, 1952, p. 233) and these therefore had very little opportunity to base a re-description on an authentic Linnaean 'type'. Hence the entomologists of the first decades after Linné were in a worse, and not in a better, situation than those of our time concerning the interpretation of the Linnaean names.

The correct application of a Linnaean binomial name on a unit considered by a modern specialist to be a 'species' encounters three main difficulties :

(a) In the *first* place, Linné's concept of the 'species' was wider than ours. In the same way as his 'genera' usually are equivalent to what we consider as families, his 'species' often include a species group, or even a whole genus. Bearing this in mind, it seems absurd that Linné should have regarded as separate species: *Pterostichus* (*Poecilus*) *cupreus* and *coerulescens*, or *Bembidion* (*Peryphus*) *ustulatum* and *rupestre*, all passing as Linnaean species in current literature. On the other hand, in some cases he happened to describe the same species twice, or even three times, under different names but this, as assumed by Roeschke (1907, p. 117 a.f.) in the case of *Tenebrio caraboides* (1758) and *rostratus* (1761) (= *Cychrus*), could probably be explained by Linné having lost (or never having possessed in his collection) the specimen first described and therefore being unable to make a direct comparison when the species again came to his notice.

(b) In the *second* place, Linné never designated any specimen as 'type'. Whether the description was based on one single or on several specimens, it cannot even be taken for granted that this (these) were preserved in his collection. Or, the original specimen may later have been substituted by another, in better condition, by Linné himself.

(c) In the *third* place, it is very difficult, often impossible, to decide if a specimen of the Linnaean collection in London is authentic or not. Linné's son, Carl Jr., who was his successor, inherited his collections and enlarged them, also with foreign specimens. J. E. Smith, who purchased them after the death of Linné Jr. (*vide* Jackson, 1888), apparently rearranged them and at any rate added many new specimens, most of them emanating from England. Attempts have been made to distinguish these from the true Linnaean insects, *e.g.* on the types of pin used, but the reliability of this method is uncertain. Originally the insect collection was apparently arranged according to the 10th edition of *Systema Naturae* (1758) by Linné himself. Of the species described in this work, if present, one or two specimens are pinned through a label in Linné's handwriting, containing not only the species name, but also its number of 1758. These specimens, especially if single, are more likely to represent true Linnaean types than any others. Species described after 1758, if represented in the collection, are unnumbered and their labels often written in a different hand.

All things considered, the Linnaean *description*, not only the first valid one but also possible supplements in his later works as well as the non-binomial of 1746, has the greater importance for fixing his species. In case the description is insufficient the specimens proposed or believed to be authentic may help in the choice between two or more related species. If description and 'authentic specimen' disagree, however, the former is decisive.

Apart from studies of details, the Linnaean collection of Carabids in London has been publicly revised three times, by F. W. Hope (1838), H. Schaum (1847) and V. Motschulsky (1855). The results which these authors obtained are in part

* It is true that Fabricius as a young man spent two years (1762-64) with Linné in Uppsala (Schuster, 1928, pp. 1 a.f., 91) but this seems to have had only little influence on his concept of the Linnaean species, at least as far as Carabids are concerned.

contradictory and will be mentioned below only where they deviate from my own. On the whole, it was not my intention to write a historical review of the various fates which the Linnaean names of Carabids have undergone in the course of time. The main purpose was only to fix for future use the original content of the Linnaean specific names, *making as few changes of current practice as possible*. Therefore, if his name *can* be interpreted in accordance with present use, I have preferred to preserve this, even if the *probability* speaks in favour of a different application. Only in cases where Linné's description is in clear *opposition* to the present use of the name is a change inevitable. Fortunately, as will be seen below, this is a situation concerning no more than four species.

I studied the Linnaean collection in London rather superficially in August 1952 and again, more thoroughly, in June 1954. I am highly indebted to Mr. W. H. T. Tams, of the British Museum (Natural History), who introduced me to the Linnaean Society on both occasions and helped me concerning the identification of 'Linnaean' pins of the insects, as well as to the officials of the Society who permitted the study. The more or less certain Linnaean specimens preserved at the Zoological Institute of the Uppsala University as well as at the Riksmuseum of Stockholm (including the De Geer collection) were studied in 1954. The so-called Linnaean collection in Uppsala was rearranged by P. Thunberg and only for specimens belonging to species described in 1764 is there clear reason to believe in authenticity.

THE SPECIES.

The species are here treated under the genus name used by Linné but otherwise in alphabetical order. The specimens preserved in the London collection are always enumerated from left to right and, if arranged in more than one transverse row, this is indicated. The specimen named here in the first place is therefore always the one standing through (or at least closest to) the name label. The probability of this specimen being an authentic Linnaean one is always greater than for the others and in fact it is often the one best matching Linné's description.

GENUS *ATTELABUS*, 1758 (1736).

A. melanurus, 1767 (p. 620). No authentic specimen preserved (but *vide* next species). The description and the provenance (Uppsala) confirm the current use of the name (*Odacantha melanura*).

A. pensylvanicus, 1767 (p. 620). A quite mutilated specimen, without head and prothorax, completely encrusted by dirt and mould, pinned through a name label in Linné's hand. After cleaning it proved to belong to the preceding species. The confusion of labels is understandable from the poor condition of the insect. The description, including provenance, can be applied to *Colliuris* (*Casnonia*) *pensylvanica* auct. only; *ludoviciana* Sallé is sufficiently excluded by colour characters.

A. surinamensis, 1767 (p. 619). Lacking in the London as well as in the Uppsala collection. The typical specimen(s) was collected in Surinam by Daniel Rolander who, to the great annoyance of Linné, submitted the main part of his collections to Ch. De Geer. Actually, De Geer described and figured the species under the Linnaean name (1774, pp. 80-81, Pl. 17, figs. 16-18; *Colliuris*). Therefore Linné's type probably had the same fate as that of *Carabus americanus* (*vide* below) with the difference that this is still in the De Geer collection (Riksmuseum, Stockholm). Now, in the general collection of this museum I found a specimen labelled "*surinamensis* Dalm." and "Mus. Payk.". This agrees so completely with De Geer's drawings, even in the carriage of the head and prothorax (which is individual and accidental), that I am inclined to believe that it is the very same specimen. If so, it may very well be the type of Linné. Paykull was notorious for not being able to master his hands when touching other people's collections and it may well be that the specimen in question passed over from De Geer's collection to his own and then, in 1819, the entire Paykull collection was bestowed on the Swedish Academy

of Science. This was the foundation of the Riksmuseum, the first keeper of which was J. W. Dalman (which may explain his name on the label). The modern interpretation of *Colliuris surinamensis* L. was fixed by Liebke (1930, pp. 669, 689). A comparison with two specimens in Mus. Univ. Berlin from Cayenne, identified by Liebke, proved to be conspecific with the supposed authentic specimen from "Mus. Payk."

GENUS *CARABUS*, 1758 (1736).

C. americanus, 1758 (p. 415; 1767, p. 671). One ♀ present. The name label is "*americanus* Fab." (with "Fab." later expunged in pencil) and lacks a number, though the description was made in 1758 (*vide* above, p. 326), which all induces doubts as to the authenticity. This specimen, as already stressed by Schaum (1847, p. 316), is the North American *Galerita janus* F. (*americanus* F. & Dej.; *vide* Lindroth, 1955, p. 22). Linné, in 1758 as well as in 1767, gives the provenance as "America" (Rolander) but De Geer (1774, p. 107) who likewise mentions Rolander as the collector, Surinam. In the De Geer collection (Swedish Riksmuseum) a ♀ is present which, for reasons given above (under *Attelabus surinamensis*), is probably the Linnaean type. This is the South American species usually passing as *Galerita americana* L. and apparently conspecific with *geniculata* Dejean (1831, p. 297), as supposed by this author himself. A comparison between the assumed Linnaean type and the typical couple of *geniculata* (♂ Guadeloupe, ♀ Cayenne; Mus. Paris) revealed no other differences than that in the former only the two, in both of the latter the four basal joints of the antennae are more or less darkened. But, as pointed out by Chaudoir (1861, pp. 555-556; 1877, pp. 254-255), the colour characters are of little value in this group of species. I studied the internal sac of the penis* in a ♂ of the true *americana* L. from Guadeloupe (*loc. class.* of *geniculata* Dej., and coloured as the type; Swed. Riksmus.) compared with a ♂ from Rio de Janeiro (identified as "*americana* L." by Liebke; Brit. Mus.) and with a ♂ of the very similar "var. c" of *nigra* Chev. (Brit. Mus.), described and figured by Bates (1883, p. 165, Pl. 6, fig. 23) (fig. 1). The internal sac of the specimen from Rio is characterized by a strongly chitinated, pineapple-like body which in the true *americana* is much less developed, in *nigra* absent. There are also differences in the extreme apex of penis as well as in the form of the rudimentary, coalescent right paramere.

C. atricapillus, 1758 (p. 416; 1767, p. 673). Described from Germany. One specimen, the label without a number (though described in 1758!) and with species name *not* in Linné's hand. It is therefore probably not an authentic specimen. The description (identical in 1758 and 1767), a simple one-line diagnosis only, could as well be applied to *Demetrias monostigma* Sam. or *Dromius melanocephalus* Dej. but the name "*atricapillus*" certainly aims at the pilosity of elytra, peculiar to *Demetrias atricapillus* auct., and to this belongs the London specimen.

C. auratus, 1761 (p. 219; 1767, p. 669). Motschulsky (1855, p. 67) says: "Je ne l'ai pas trouvé dans la Col. de Linné", which is difficult to understand as, actually, three specimens are present, of which one is *auratus* auct., pinned through the label, and on each side one *monilis* F. (*f. typ.*), both marked "Anglia". The first-named specimen may be authentic, though it is not necessarily so. At any rate the description of the elytral carinae as "non interruptis, nec nigris" fits *auratus* auct. only. But the provenance, in 1761 given as "Suecia", is probably wrong; the species has never since been found in Sweden. As pointed out by Motschulsky (*l. c.*), the picture in *Pandora Insectorum* (1758) given as *nitens* seems to represent *auratus*, which probably at that time was included in Linné's concept of *nitens* (*vide* below).

C. bimaculatus, 1771 (p. 552). Two specimens present, completely agreeing with the long series under *Pheropsophus bimaculatus* in the general collection of the

* In *Galerita*, the penis must be boiled in 15 per cent KOH and after careful washing in water transferred (*via* absolute alcohol) into clove oil, in order to allow a detailed study of the internal sac.

British Museum. It was re-described by Chaudoir (1876, p. 34). Concerning the correct application of the name, *vide* Andrewes (1919, p. 120; 1921, p. 153; 1923, p. 460). It seems impossible to decide whether the two specimens of the Linnaean collection are 'types' (as proposed by Andrewes, 1919, 1923) or not, but it is permissible to use the name according to practice. Linné gives no *terra typica* but refers to Fabricius, from whom he probably got his specimen(s). Fabricius later (1801, p. 217, *Brachinus*) reported the provenance as "India orientalis".

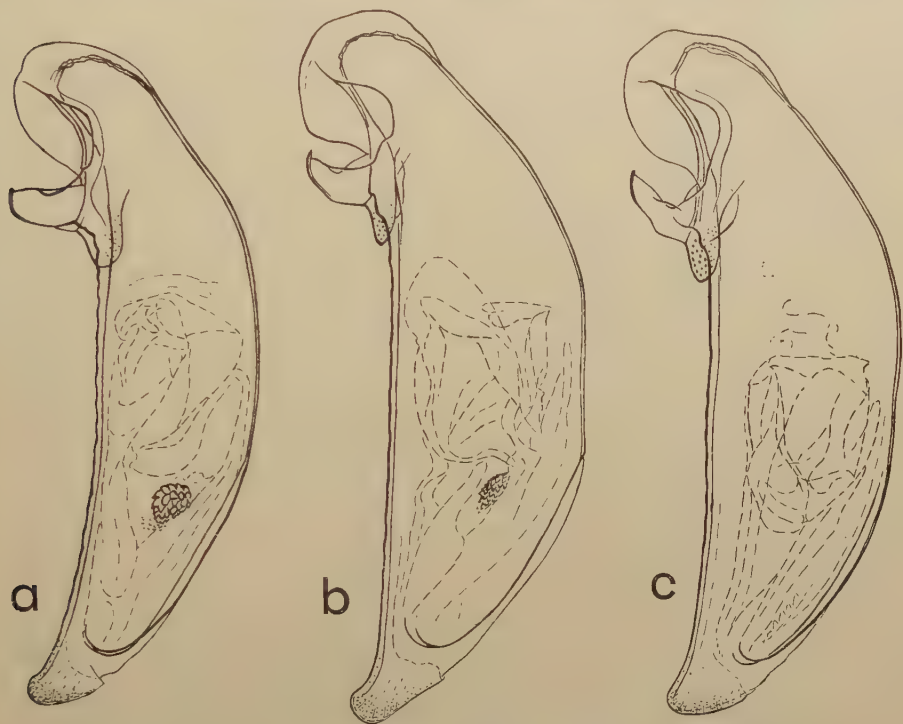


FIG. 1.—Penis and coalescent right paramere in *Galerita*.

(a) *G. sp.* (Rio de Janeiro; identified as "*americana L.*" by M. Liebke); (b) *G. americana L.* (Guadeloupe; compared with the proposed Linnean type in the De Geer collection); (c) *G. nigra* Chev., "var. c", Bates (Guatemala).

C. bipunctatus, 1761 (p. 223; 1767, p. 672). It is difficult to understand how Motschulsky (1855, p. 63) could declare: "Le type dans la Col. de Linné est un *Ag.* (= *Agonum*) *parumpunctatum* (= *Mülleri* Hbst.)". Of the three specimens present nos. 1 and 3 are *Bembidion* (*Testedium*) *bipunctatum* auct., no. 2 *B.* (*Metallina*) *properans* Steph. The description ("elytris punctis duobus impressis") refers to the first-named species. A rearrangement of the specimens after Motschulsky's visit (probably in 1853) seems highly improbable and, besides, Linné's description ("corpus vix pediculo majus") fits no *Agonum*.

C. buprestoides, 1767 (p. 670). "*Europa australis.*" No specimen present. As already stated by Hope (1838, p. 53), this name cannot be interpreted. The words "*caput a thorace receptum*" seem to exclude any member of the Carabid family. Fabricius (1792, p. 234) described an *Elater buprestoides* (= *Xylita b.*), with the remark: "*ab E. buprestoides* Linn. (= *Melasis b.*) omnino diversus"; but, by chance, the *Xylita* is one of the insects best fitting Linné's description of *Carabus buprestoides*.

C. caeruleus, 1758 (p. 416 ; 1736, p. 116, *Buprestis* no. 8 ; 1746, p. 173, no. 520; 1761, p. 222 ; 1767, p. 672). Three specimens : no. 1 (pinned through the label) = *Pterostichus* (*Poecilus*) *cupreus* auct. ; no. 2 = *Harpalus affinis* Schrk. (*aeneus* F.) ; no. 3 = *Pter.* (*Poec.*) *coeruleus* auct. Specimens 1-2 have Linnaean pins, no. 3 a more modern pin. The first valid description (1758 : "nigro-caeruleus, antennis basi rubris") gives no criterion at all for an identification and Linné on this occasion does not refer to the earlier description of " (*Carabus* supra *aeneus*, etc." (1746). This in its turn, without any doubt applies to *Pterostichus* (*Bothriopterus*) *oblongopunctatus* F. ("coleopteris punctis sex excavatis" and "femora nigra : tibiae rufae"). On the other hand, Linné's failure to cite the first edition of *Fauna Suecica* does not necessarily mean that he doubted the identity ; *C. crux major* and *C. hortensis* of 1758 were likewise given without any reference to 1746. In 1761, however, Linné combined the two earlier descriptions but introduced the species of 1746 as a varietas β of the *caeruleus* of 1758. He gives different 'diagnoses' but the single 'description', which ought to have been common to both forms, repeats the features characterizing *Pterostichus oblongopunctatus*. In 1767, finally, the poor diagnosis of 1758 is unchanged. The matter is thus utterly confused : the *forma typica* of *caeruleus* (in 1758 as well as in the following works) may be specifically distinct from the var. β of 1761 (*P. oblongopunctatus*) but on the other hand it may be based on unusually metallic specimens of the latter. At any rate there is no reason at all to identify it with *P. coeruleus* auct., partly because Linné would never have kept this separate from *cupreus* L., auct. (*vide* below). This distinction was first made when Sturm (1824, p. 99) described his *versicolor*. The only satisfactory solution is to drop the Linnaean name *caeruleus* and to replace it in its present sense by *versicolor* Sturm. G. H. Horn (1878, p. 29), without argumentation, made the mysterious identification of *caeruleus* with *Loricera pilicornis* F., later adopted by Csiki (1927, p. 433) who, in spite of this, at the same time kept the Linnaean name, with identical reference to 1758, for *Pterostichus coeruleus* auct. (*l. c.*, 1930, p. 590).

C. cephalotes, 1758 (p. 414 ; 1761, p. 220 ; 1767, p. 669). Three specimens, all = *Broscus cephalotes* auct.

C. clatratus, 1761 (p. 218 ; 1767, p. 669). The single specimen is labelled "clathratus", and not in Linné's hand, but the description is sufficient (= *Carabus clathratus* auct.). The change of spelling is dubious but generally accepted.

C. complanatus, 1767 (p. 671). Described from Spain. Two specimens, no. 2 marked "Swansea, Leach", and thus not Linnaean. The first specimen may be the actual type and the description is anyhow sufficient : = *Eurynebria complanata* auct.

C. coriaceus, 1758 (p. 413 ; 1767, p. 668). Described from Germany. Two specimens : = *Carabus* (*Procrustes*) *coriaceus* auct.

C. crepitans, 1758 (p. 414 ; 1761, pp. 220-221 ; 1767, p. 671). Two specimens : no. 1 is *Brachynus crepitans* auct., no. 2 a large, probably North American species, possibly *B. fumans* F. (Hope, 1838, p. 55 ; Schaum, 1847, p. 316) ; but the *Brachynus* species of that continent are still in a state of taxonomic confusion. Linné described the species from Sweden, quoting Rolander (1750), and the first specimen may be the 'type'.

C. crux major, 1758 (p. 416 ; 1736, p. 115, *Necydalis* no. 3 ; 1746, p. 153, no. 439, *Chrysomela* ; 1761, p. 223 ; 1767, p. 673). One specimen = *Panagaeus crux-major* auct.

C. crux minor, 1758 (p. 416 ; 1761, p. 223 ; 1767, p. 673). One specimen = *Lebia crux-minor* auct.

C. cupreus, 1758 (p. 416 ; 1761, p. 222 ; 1767, p. 672). Two specimens : no. 1 = *Amara aenea* De G. ; no. 2 = *Pterostichus* (*Poecilus*) *coeruleus* auct. (*versicolor* Sturm). The first-named species, which possesses three distinctly pale basal joints of antennae, must be excluded (1761 : "Antennarum primus articulus saepius ruber est"). Linné's diagnoses and the short description of 1761 are very indifferent and the separation from *caeruleus*, with which it was compared in 1761, is founded on the brighter metallic colour only. This induced Motschulsky (1855, p. 60) to

regard both as conspecific. As stressed above, under *caerulescens*, there is no reason to regard this as a *Poecilus* but *cupreus* certainly is. In the collection of De Geer (Swed. Riksmus.), who was in intimate contact with Linné, three specimens of *coerulescens* auct. (*versicolor* Sturm) stand under the label "*cupreus* L.". It is justifiable to regard *cupreus* L. as a collective species including both the true *cupreus* auct. and *versicolor* Sturm and to preserve the name for the first-mentioned, according to practice.

C. cyanocephalus, 1758 (p. 415; 1746, pp. 173-174, no. 525; 1761, p. 221; 1767, p. 671). Three specimens, nos. 1 and 3 = *Lebia cyanocephala* auct., no. 2 = *L. chlorocephala* Hoffm. Motschulsky (1855, p. 50) identified the Linnaean species with the latter. Linné, no doubt, regarded them as conspecific and the 'diagnosis' of 1758 ("pedibus ferrugineus") suggests *chlorocephala* but the 'description' of 1746 (unaltered in 1761), to which Linné referred in 1758, fits *cyanocephala* auct. alone ("pedes ex rubro & nigro varii"). The name should therefore be used as hitherto.

C. decemguttatus, 1764 (p. 96; 1767, p. 669). Described from the Cape Colony. Three specimens in the London collection, one specimen in Uppsala (ex Mus. Lud. Ulr.), all = *Thermophilum decemguttatum* auct. (Basilewsky, 1948, p. 110; 1950, p. 80). The Uppsala specimen is marked as "typ" which is wrong because only the first London specimen fits the description and the Linnaean name, in having ten elytral spots. These are short and rounded, pure white; the striae lacking conspicuous villosity (thus no ab. *villosa* Leq.); the prothorax is quite black with coarse and moderately dense punctuation (thus no "sbsp. *quadriguttatum* F."). Length 35 mm.

C. fastigiatus, 1764 (p. 97; 1767, p. 670). Described from the Cape Colony. One specimen in the London collection, one in Uppsala (ex Mus. Lud. Ulr.), the latter marked as "typ", both = *Pheropsophus fastigiatus* auct.; compared with many specimens in the Brit. Mus. and one in Mus. Congo Belg. (det. Basilewsky).

C. ferrugineus, 1758 (p. 415; 1761, p. 221; 1767, p. 672). One specimen = *Leistus ferrugineus* auct. Owing to the very poor descriptions, Linné's name was formerly also used for *Amara fulva* De G. (Hope, 1838, p. 58; Motschulsky, 1855, p. 60; and many others), which stands as "*ferrugineus* L." in the De Geer collection (Swed. Riksmus.). Only Linné's words "thorace glaberrimo" and the habitat "in Sylvis" (1761) suggest *Leistus* rather than *Amara*.

C. germanus, 1758 (p. 415; 1767, p. 672). Described from Germany. One specimen = *Diachromus germanus* auct. Linné's short diagnoses are sufficient.

C. granulatus, 1758 (p. 413; 1746, pp. 170-171, nos. 511-513; 1761, pp. 217-218; 1767, p. 668). Four specimens: no. 1 = *morbillosus* F., completely agreeing with a specimen from Algeria (Mus. Lund.); no. 2 = *monilis consitus* Panz., compared with English specimens (Brit. Mus.); no. 3 = *granulatus* auct.; no. 4 = *cancellatus* Ill. Linné originally (1746) described the species from Sweden under three different diagnoses, based on differences in colour only, which were combined and referred to in 1758. Therefore Sweden must be regarded as *patria classica*, which excludes *morbillosus* and *monilis*. Possibly *cancellatus* was included in Linné's concept of *granulatus* though he ought to have noticed the red basal joint of antennae in *cancellatus*. That he never described this species is understandable, however, considering the fact that it does not occur in the Uppsala region (Lindroth, 1945, p. 140).

C. hortensis, 1758 (p. 414; 1736, p. 115, no. 1; 1746, p. 171, no. 514; 1761, p. 218; 1767, p. 668). Two specimens in the London collection: no. 1 = *hortensis* auct., no. 2 = *nemoralis* Müll.; one specimen in the Linnaean collection of Uppsala, = *nemoralis*. Linné never made a separate description of *nemoralis* and probably regarded it as conspecific with *hortensis* auct. The words "elytris . . . punctis aeneis" of the first valid diagnosis (1758) justify the present use of the name.

C. inquisitor, 1758 (p. 414; 1761, p. 220; 1767, pp. 669-670). Four specimens (no. 4 a later addition, from Wales), all = *Calosoma inquisitor* auct. The descriptions are sufficient.

C. intricatus, 1761 (p. 217; omitted in 1767!). "Succia & Germania" are given as patriae but, though the species was recently discovered in Scania (Brinck, 1942), the former record is probably false; Germany should be regarded as *terra typica*. One specimen=*intricatus* auct.

C. latus, 1758 (p. 415; 1736, p. 117, *Buprestis* no. 9; 1746, p. 173, no. 521; 1767, p. 672; omitted in 1761). Six specimens, in three rows:

1st row: no. 1=*Harpalus Winkleri* Schaub. (♀); no. 2=*Agonum Mülleri* Hbst.

2nd row: no. 3=*Amara apricaria* Payk.; no. 4=*Amara aeneu* De G.

3rd row: nos. 5 & 6=*Harpalus affinis* Schrk. (*aeneus* F.).

In this mixture of species only specimens nos. 1 and 3 tolerably fit the description but preference must be given to the *Harpalus* because the *Amara* can hardly be termed "ater" (1746) or "niger" (1758, 1767). Fabricius (1801, p. 196) used Linné's name for *Amara apricaria* Payk. and Gyllenhal (1810, p. 133) for another member of subgenus *Bradytus*, *consularis* Dft. Schaum (1847, p. 317) and Motschulsky (1855, p. 44), who considered the first specimen only, both identified it wrongly, the former as *latus* auct., the latter, with some doubt, as the North American *herbivagus* Say, apparently seduced by Linné's alternative patria record (1758, 1767), *America septentrionalis*. Now, Linné would certainly have regarded *latus* and *Winkleri* (and other similarly coloured members of the genus *Harpalus*) as conspecific; his "*latus*" is a pronounced collective species. The record in 1746, "apud nos vulgaris", cannot aim at *Winkleri*, which is rare in Sweden, and it is due only to an unfortunate chance that a specimen of this species has been preserved as 'type'. It seems quite justifiable to use *latus* L., according to practice, for the species of the group which is by far the commonest in Sweden.

C. leucophthalmus, 1758 (p. 413; 1746, p. 171, no. 515; 1761, pp. 218-219; 1767, pp. 668-669). Two specimens, both=*Sphodrus leucophthalmus* auct. The name was long used for *Pterostichus melanarius* Ill. (*vulgaris* auct.), apparently because Linné (in 1761) described his species as "apterus". This was probably a pure mistake (not repeated in his other descriptions of the species) and he described the *Pterostichus* mentioned under *Carabus vulgaris* (*vide* below). Thomson (1859, p. 233) has given the reasons why *leucophthalmus* L. is less likely to be referred to *Sphodrus*. I think it is justifiable, in this case, to accept the specimens of the London collection as authentic (no. 1 is labelled "3 *leucophthalmus*", in Linné's hand) and to admit that Linné may have mixed in a *Pterostichus* (*niger* Schall. rather than *melanarius* Ill.) under his concept of the species.

C. lividus, 1758 (p. 414; 1761, p. 220; 1767, p. 670). One specimen=*Nebria livida* auct. (*forma typica*, with broadly pale margins of elytra). The descriptions are sufficient.

C. marginatus, 1758 (p. 416; 1761, p. 220; 1767, p. 670). Two specimens, =*Agonum marginatum* auct. Hope (1838, pp. 54, 73) remarked that Linné had confused the species mentioned with the similarly coloured *Chlaenius vestitus* Payk. The description of 1767 fits only the latter ("antennae ferrugineae", "elytra . . . pubescentia") but both of the earlier descriptions say "antennae nigrae", which applies to the *Agonum*.

C. melanocephalus, 1758 (p. 415; 1746, pp. 173, 174, nos. 524, 526; 1761, p. 221; 1767, p. 671). One specimen=*Calathus melanocephalus* auct. The description is sufficient.

C. meridianus, 1761 (p. 221; 1767, p. 673). Three specimens: nos. 1 and 2 =*Acupalpus meridianus* auct., no. 3 =*Bembidion properans* Steph. The description fits only the former and is sufficient, except that dark forms of *A. dorsalis* F. would also agree and that, in both species, the base of antennae should be termed "ferrugineus".

C. multipunctatus, 1758 (p. 416; 1761, p. 223; 1767, p. 669). Four specimens, all=*Blethisa multipunctata* auct. The descriptions are sufficient.

C. nitens, 1758 (p. 414 : 1736, p. 115, no. 2 ; 1746, p. 172, nos. 517, 518 ; 1761, p. 219 ; 1767, p. 669). Four specimens, arranged in two rows : nos. 1 and 2 = *nitens* auct., nos. 3 and 4 = *auratus* auct. (one labelled Switzerland, apparently a later addition). In 1746, Linné described two different species (nos. 517 and 518) which were combined under *nitens* in 1758 (and 1767) ; but in 1761, he repeated the two original detailed descriptions of 1746 and placed no. 518 as a var. β under no. 517 (the true *nitens*). The most important differences mentioned are :

nitens, s. str.
(1746, no. 517)

nitens, var. β
(1746, no. 518)

- (a) totum corpus viridi nitens.
- (b) convexitates (i.e. carinae elytrorum) magis obscurae sunt, non tamen nigrae sed potius magis caeruleae.
- (c) totus viridis est.
- (d) pedes & antennae in aliis ferruginea s. testacea.
- (e)

- (a) corpus totum nigrum subtus.
- (b) convexitatibus nigris.
- (c) margo elytrorum exterior ignei coloris est.
- (d) pedibus antennisque nigris.
- (e) antennis dimidio brevioribus.

Actually, var. β comprises an excellent description of *Carabus nitens* auct. But no. 517, the 'true' *nitens*, is a different species. It has often been interpreted as *auronitens* F. (also by Breuning, 1932-37, pp. 1468, 1482), which does not occur in Sweden.* To my mind, however, it is *auratus* auct. The reasons are : (1) this species, but no *auronitens*, is present under *nitens* in the London collection ; (2) the picture of "*nitens*" given in *Pandora Insectorum* (1758) seems to be *auratus* ; (3) the description of no. 517 in 1746 (repeated in 1761) fits *auratus* better than *auronitens*, especially in the points (b) and (d) above.

The case can probably be reconstructed in the following way. After Linné, in 1758, had combined nos. 517 and 518 of 1746, he again discovered that they were different and, in 1761, described no. 517 as *auratus*. He forgot, however, to remove the corresponding half from the description of *nitens*, which was simply and automatically copied from 1746. The fact that two specimens of *nitens* auct. stand on the first place in the Linnaean collection (though they should belong to his var. β) may probably be explained by Linné afterwards becoming aware that he had already described the other of his two *nitens*-forms as *auratus*. It is also puzzling that no. 517, i.e. *auratus*, was reported from the island of Öland, where it certainly does not occur, though the reference to "Iter Oelandicum" was given under no. 518, i.e. *nitens* auct., which is a very characteristic insect for the steppe-like 'alvar' of the island.

The first valid description of *nitens* (1758), fortunately, makes no distinction between the two forms. It is a collective species and it is permissible, according to practice, to select the present *nitens* auct. as the type notwithstanding that Linné on a later occasion (1761) regarded it as a variety. It is also worth mentioning that *auratus* has never been observed in Sweden in recent times so that its inclusion in the two editions of *Fauna Suecica* (1746, 1761) is probably due to a wrong patria record.

C. piceus, 1758 (p. 416 ; 1761, p. 222 ; 1767, p. 672). Two specimens : no. 1 = *Agonum* (*Europhilus*) *piceum* auct. ; no. 2 = *Agonum* (s. str.) *ericeti* Panz. Only the first-named fits the description. Motschulsky (1855, p. 63) wrongly identified it as *A. (E.) Thoreyi* Dej. ("pelidnum"). Linné's description is quite insufficient but the name may be used according to practice.

* Fabricius (1792, p. 129) described *auronitens* from Germany (Saxonia) and not from Sweden, as erroneously stressed by Breuning (1932-37, p. 1482).

C. quadrimaculatus, 1758 (p. 416 ; 1761, p. 224 ; 1767, p. 673). One specimen = *Dromius quadrimaculatus* auct. (two additional specimens from England, one conspecific, the second = *Bembidion* (*Nepha*) *Genei Illigeri* Net.). The description of 1761 is very good.

C. quadripustulatus, 1761 (p. 224 ; 1767, p. 672). I could find no specimen, nor could Schaum (1847, p. 317) ; but Motschulsky (1855, p. 51) reported that he had seen the species in the Linnaean collection and that it was *Mycetophagus quadripustulatus* auct., as generally accepted. Possibly it has been removed from the Carabid boxes of the collection. Linné himself (1761) had observed the foreign appearance of this "*Carabus*": "*Elytrorum declivitas & Antennae obtusiusculae primo intuitu a Carabis alienum reddunt*".

C. sexpunctatus, 1758 (p. 416 ; 1736, p. 116, *Buprestis* no. 6 ; 1746, p. 172, no. 519 ; 1761, p. 223 ; 1767, p. 672). Four specimens : nos. 1-3 = *Agonum sexpunctatum* auct., no. 4 = *Loricera pilicornis* F. The description (1746, 1761) is quite sufficient.

C. spinipes, 1758 (p. 415 ; 1761, p. 221 ; 1767, p. 671). No specimen could be found by me, nor by Schaum (1847, p. 316), but Motschulsky (1855, p. 59) reported to have seen "le type, conservé dans la Col. de Linné, à Londres", and that it is *Amara* (*Cyrtotus*) *aulica* Panz. (1797). The same view had already been taken by Gyllenhal (1810, p. 101), Dejean (1828, p. 515), Schioedte (1841, p. 167), and later by Thomson (1859, p. 238), whereas Paykull (1806, p. 181) made this interpretation with doubt only. Linné gives no description, only a very short diagnosis which cannot be interpreted. That Motschulsky claimed to have seen the 'type' (possibly also Hope, 1838, p. 56) is no sufficient reason for reviving the Linnaean name.

C. sycophanta, 1758 (p. 414 ; 1761, p. 220 ; 1764, p. 95 ; 1767, p. 670). Two specimens : no. 1 = *Calosoma sycophanta* auct. ; no. 2 (labelled "Allen") = *C. scrutator* F., from North America. There is also one specimen in Mus. Uppsala (no doubt the one published in 1764), = *C. sycophanta* auct. The description (incl. patria) is quite sufficient.

C. testaceus, 1761 (p. 224 ; 1746, p. 173, no. 523 ; 1767, p. 673 ; omitted in 1758). No specimen present, nor do any of the previous students of the London collection seem to have discovered the species. It is not present in the De Geer collection (Swed. Riksmus.) and not mentioned in his *Mémoires*, though Linné (in 1746) referred to De Geer (probably as the actual author). Following Fabricius (1801, p. 209) and Gyllenhal (1810, p. 36), several authors have interpreted the species as *Trechus* (*Epaphius*) *secalis* Payk. but the reported size ("mediae magnitudinis") seems to make this impossible. Motschulsky (1855, p. 51) suggested *Dromius linearis* Ol., which at least fits the *testaceus* of Fabricius better, as this was described as "alatus". Linné's sentence: "*Elytra absque punctis & striis*", to my mind points to a beetle not belonging to the Carabid family. The name should be disregarded.

C. truncatellus, 1761 (p. 224 ; 1767, p. 673). One specimen, = *Metabletus truncatellus* auct. It is very remarkable that the size is given as "*vix Cimice major*", and "*magnitudo Cimicis*", but otherwise the description seems to fit a *Metabletus* very well. It is permissible to use the name according to practice.

C. ustulatus, 1758 (p. 416 ; 1746, p. 174, no. 528 ; 1761, p. 224 ; 1767, p. 673). Six specimens : no. 1 = *Bembidion* (*Eupetedromus*) *dentellum* Thunb. ; nos. 2 and 4 = *B. (Peryphus) ustulatum* auct. ; no. 3 = *B. (Notaphus) varium* Ol. ; no. 5 = *Chlaenius tristis* Schall. ; no. 6 (in a second row) = *Amara apricaria* Payk. The two last-named should be entirely disregarded. The authors of the early 19th century used the Linnaean name for all three species of *Bembidion* mentioned above, and also for *B. (Notaphus) obliquum* Sturm and *B. (N.) semipunctatum* Don. (vide Csiki, 1928, pp. 56-67, 116). The present interpretation of the name as aiming at a *Peryphus*, unfortunately cannot be maintained. The expressions "*fascia ferruginea*" (1746) and "*bifasciatis*" (1758, 1761, 1767) for the pale elytral spots, can only be applied to a *Bembidion* of the subgenera *Eupetedromus* or *Notaphus*, though the remark :

"non raro etiam macula pallida versus basin in exteriore parte elytri" (1761) suggests that *ustulatum* auct. may have been included as a variety. Linné certainly included both *dentellum* Thunb. (perhaps even *tinctum* Zett., vide Lindroth, 1944) and *varium* Ol. in his concept of *ustulatum*. No decision can be made from the description nor from the fact that a specimen of *dentellum* now stands on the first place in the Linnaean collection. The application of the name *ustulatum* to any of these two species would moreover cause hopeless confusion for decades. I propose to drop the name "*ustulatum* L." altogether and to substitute *ustulatum* auct. with the oldest of the indisputable synonyms, *tetracolum* Say, 1823 (p. 89; vide Fassati, 1950).

C. vaporariorum, 1758 (p. 415; 1746, p. 174, no. 529; 1761, p. 221; 1767, p. 671). Two specimens: no. 1=*Cymindis vaporariorum* auct.; no. 2=*Agonum dorsale* Pont. Only the first-named may fit the description. Gyllenhal (1810, p. 162) has pointed out that the species of 1761 ("vix pediculo duplo majore", and "sutura longitudinalis grisea"; repeated from 1746) is probably an *Acupalpus*, whereas the species of 1767 ("*C. meridiano* quadruplo major") may be a *Cymindis*. The concept of 1758, the first valid, seems to be a pronounced collective one, but whether the *Cymindis* was included already on that occasion is at least doubtful. The association with *Stenolophus teutonius* Schrk. (*vaporariorum* F.) is preposterous as this does not occur in the Uppsala region from where Linné described his *vaporariorum* (vide Schioedte, 1841, p. 149). The present use of the name, founded first and foremost on the Linnaean 'type', has a slight foundation and its conservation is here recommended mainly for reasons of stability.

C. velox, 1761 (p. 222; 1746, p. 173, no. 522; 1767, p. 672; omitted in 1758). No specimen present but the descriptions, including those of the habitat and behaviour, are clear. It is *Bembidion* (*Chrysobracteum*) *velox* auct.

C. violaceus, 1758 (p. 414; 1736, p. 115, no. 3; 1746, pp. 171-172, no. 516; 1761, pp. 219-220; 1767, p. 669). Two specimens (no. 2 marked "Anglia, Jones"), both=*Carabus violaceus* auct. The descriptions are sufficient.

C. vulgaris, 1758 (p. 415; 1746, nos. 527 and 530; 1761, p. 222; 1767, p. 672). Four specimens: nos. 1, 3 and 4=*Pterostichus* (*Omaseus*) *melanarius* Ill. (*vulgaris* auct.); no. 2=*P. (Lyperosomus) aterrimus* Hbst. This Linnaean name has caused much inconvenience. Since Schaum (1847, p. 317) had discovered that three of the four specimens of the Linnaean collection belong to the *Pterostichus* first mentioned, this has generally passed as *vulgaris*. But already Hope (1838, pp. 58, 86) realized that Linné's description in 1758 ("nigro-aeneus"), as well as that of the *forma typica* in 1767, cannot be applied to this *Pterostichus*. The name *vulgaris* had also long been used for different species of *Amara* (vide Schioedte, 1841, p. 187; Csiki, 1929, pp. 408-420, 435).^{*} Quite recently, Andrewes (1939, p. 184) revived this custom and applied the name to *Amara* (s. str.) *lunicollis* Schioe., which is completely arbitrary. Indisputably, no. 530 of 1746, made the var. β of *Carabus vulgaris* in 1761 and also included under this name in 1767, is *Pterostichus melanarius* Ill. (*vulgaris* auct.) or at least included this species. That Linné would have regarded this as a 'variety' of an *Amara*, only half as long, is completely out of the question. Only the colour is given as a distinguishing character, which means that the "*forma typica*" ought to have been based on a species of about the size of *Pterostichus melanarius* and like this with dark (or at most basally diffusely paler) antennae, but with metallic reflection of the upper surface. The insect best meeting these requirements seems to be *Pterostichus* (*Poecilus*) *lepidus* Leske. It is therefore interesting to find that De Geer, Linné's contemporary with whom he was in closest contact, had a *Poecilus versicolor* Sturm (*coerulescens* auct.) under the name of "*Carabus vulgaris* L." in his collection and that the description of his "*Carabé vulgaire*" (1774, pp. 97-98) fits *P. lepidus* best. This interpretation, however, is merely a probability; *inter alia* the sentence: "Variat punctis impressis in elytris,

^{*} It was therefore quite a matter of logic when Paykull (1798, p. 167) interpreted Linné's *Carabus vulgaris* var. β as *Oodes helopioides* F.

& non impressis" (1746 ; N.B. for the metallic form, the later *forma typica* !), leads to the speculation that *Pterostichus oblongopunctatus* F. may have been included in Linné's *vulgaris*. After all, this name must be regarded as uninterpretable and should be omitted for the future.

GENUS *CICINDELA*, 1758 (1736).

C. aequinoctialis, 1763 (p. 395 ; 1767, p. 658). Two specimens below a label "*? equinoctialis*" (not in Linné's hand). Both specimens are pinned through a label marked "Calcutta". No. 1=*Pheropsophus bimaculatus* L. (with unusually reduced transverse yellow band of elytra) ; no. 2, apparently, is likewise an Indian species, almost certainly *Ph. Catoirei* Dej. Linné described *aequinoctialis* from Surinam (probably collected by Rolander). The two specimens above are therefore not authentic and probably Linné never possessed the species in his own collection (*vide* above, *Attelabus surinamensis*). A confirmation of the correct application of the name in present use is therefore impossible, the more as the species has been split into a number of 'varieties' (Chaudoir, 1876, p. 45 ; Hubenthal, 1914, pp. 445-447).

C. aquatica, 1758 (p. 408 ; 1736, p. 116, no. 6 ; 1746, p. 181, no. 558, *Buprestis* ; 1761, p. 212 ; 1767, p. 658). Three specimens : nos. 1 and 2=*Notiophilus biguttatus* F., no. 3=*N. Germinyi* Fauv. (*hypocrita* auct.). Linné, no doubt, regarded all *Notiophilus* as one species but if he had *biguttatus* before him when writing the description it is difficult to understand that he overlooked the pale apex of elytra. The statement "*pedes nigrae*" (1746, 1761) would also, strictly interpreted, exclude *Germinyi*. It must be regarded as justifiable to use the name for *Notiophilus aquaticus* auct.

C. campestris, 1758 (p. 407 ; 1746, p. 178, no. 548 ; 1761, p. 210 ; 1767, p. 657). Four specimens (nos. 3 and 4 labelled "Anglia"), all=*Cicindela campestris* auct. The description is sufficient.

C. capensis, 1764 (p. 84 ; 1767, p. 657). Described from the Cape Colony. It was also described and figured by De Geer (1778, pp. 628-629, Pl. 47, figs. 3-4). Three specimens : nos. 1 and 2=*C. capensis* auct. ; in both the longitudinal dark stria of elytra is interrupted in front of the apical transverse band. No. 3 belongs to the multifarious *C. brevicollis* Wied. and agrees with specimens in the Brit. Mus., identified as *clathrata* Dej. var. *minor* W. Horn. This form has a more northern distribution and Linné's name should be kept for *Cicindela capensis* auct.

C. carolina, 1763 (p. 395 ; 1767, pp. 657-658). Described from Carolina, U.S.A. Two specimens, both=*Megacephala (Tetracha) carolina* auct. The description of 1763 is sufficient.

C. flavipes, 1761 (p. 211 ; 1767, p. 658). One specimen=*Asaphidion flavipes* auct. The description of 1761, though short, is sufficient.

C. germanica, 1758 (p. 407 ; 1767, p. 657). Described from Germany. Three specimens (no. 3 marked "Anglia, Lewin"), all=*Cicindela germanica* auct. The description is sufficient.

C. hybrida, 1758 (p. 407 ; 1761, p. 210 ; 1767, p. 657). Three specimens : no. 1=*Cicindela maritima* Dej. ; no. 2=*C. trisignata* Dej. ; no. 3 (labelled "Mt. Simplon, Alps")=*C. hybrida riparia* Dej. The species was almost certainly described on Swedish material and then only the specimen no. 1 may be 'typical'. It was figured by Westwood (1839, Pl. 1, fig. 1) and mentioned by him in a short article (1838, p. 342). Schaum (1847, pp. 279-280) and Motschulsky (1855, p. 30) observed that the 'type' belongs to *maritima* and so the name was used by several authors of the early 19th century (*vide* W. Horn, 1926, p. 219). Both *hybrida* auct. and *maritima* occur in Sweden and if Linné had seen both he would of course have regarded them as conspecific. The diagnoses and descriptions fit both of them equally well, only the recorded habitat "in Sylvis" (1761) seeming to exclude *maritima* ; but Linné's habitat notes of insects are generally not very reliable. For practical reasons,

and in spite of Linné's London 'type', I think it justifiable to retain the name for *hybrida* auct.

C. maura, 1758 (p. 407 : 1767, p. 658). One specimen = (*Cicindela maura* auct. The middle band of elytra is divided into two separate spots. This specimen is therefore not the one described in 1758 ("punctis . . . tertio & quarto confluentibus") from Algeria but apparently one added later (1767) from Sicily.

C. quadrimaculata, 1761 (p. 211 : 1767, p. 658). No specimen is present but, though the description would fit *Bembidion* (*Nepha*) *Genei* Illigeri Net. as well, it seems justifiable to keep the name for *Bembidion* (s. str.) *quadrimaculatum* auct.

C. riparia, 1758 (p. 407 : 1736, p. 115, no. 3 ; 1746, p. 179, no. 550 ; 1761, p. 211 ; 1767, p. 658). Two specimens : no. 1 = *Elaphrus cupreus* Dft. ; no. 2 = *E. riparius* auct. Linné no doubt regarded all *Elaphrus* as conspecific but, as pointed out by Schaum (1847, p. 280), the descriptions agree better with *riparius* auct., especially the colour, "viridi-aenea" ; also the litoral habitat "inter arenam humidam" hardly fits *cupreus*. The name may be kept according to practice.

C. rupestris, 1767 (p. 658). One specimen (without head and prothorax) = *Bembidion* (*Notaphus*) *obliquum* Sturm. Schaum (1847, p. 280) identified it as *B. (Diplocampa) fumigatum* Dft., Motschulsky (1855, p. 36) as *B. (Notaphus) varium* Ol. ("ustulatum auct.", nec L.). This case is very similar to that of *Carabus ustulatus* L. ; in both the name is generally used for a *Bembidion* of the subgenus *Peryphus* but from the descriptions and the more or less authentic specimens it is evident that the names were established on members of subgenera *Notaphus* or *Eupetodromus*. In *rupestris*, the pattern of elytra : "antice macula ferruginea, in singulis singula, postice fascia utrisque communi triloba, ferruginea", can never be applied to any *Peryphus*. On the other hand, it is impossible to decide which species of *Notaphus* was described : *semipunctatum* Don., and also *varium* Ol., may at least have been included, though the expression : "nigra, etiam pedibus", as well as the London specimen, speak in favour of *obliquum* Sturm. Now, a transmission of "*rupestris* L." to this species would cause hopeless confusion for decades. I therefore venture to propose that the Linnaean name be abandoned altogether and that the present *Bembidion* (*Peryphus*) *rupestre* auct. be substituted by its earliest valid synonym, *bruxellense* Wesmaël, 1835 (p. 47), which was long used for the species.

C. sylvatica, 1758 (p. 407 ; 1736, p. 115, no. 1 ; 1746, pp. 178-179, no. 549 ; 1761, p. 210 ; 1767, p. 658). Three specimens, all = *Cicindela sylvatica* auct. (there is no reason to change Linné's spelling). The descriptions are sufficient.

C. virginica, 1767 (p. 657). Described from Carolina, U.S.A. No specimen is present but the description, though very short, gives *Megacephala* (*Tetracha*) *virginica* auct.

GENUS *TENEBRIO*, 1758 (1746).

Only species which belong, or have been proposed to belong, to the Carabid family are treated here.

T. caraboides, 1758 (p. 418 ; 1746, p. 190, no. 595 ; 1761, p. 227 ; 1767, p. 677). Not in the London collection. In the 'Linnaean Collection' (rearranged by Thunberg!) of Mus. Uppsala there are two different exotic Tenebrionids under the label "*Sepidium caraboides*".* Linné's descriptions are short and of little significance ; only the expressions "thorax ut in Carabis" and "maxillae capitulis longitudinalina" point to *Cychnus*. This interpretation is strongly supported, however, by De Geer, who, in describing his *Carabus coadunatus* (1774, p. 92), accompanied by excellent figures (Pl. 3, figs. 13-14) showing a *Cychnus caraboides* auct., referred to Linné's descriptions of 1761 and 1767. On the other hand, Linné (1746, p. 190) referred to Tab. XXII of Frisch (1738) which shows *Broscus cephalotes* L.! It may, however, be justifiable to follow Roeschke (1907, p. 217 a.f.) and use the Linnaean

* *Sepidium* is a Tenebrionid genus set up by Fabricius (1775) but there seems never to have occurred a '*S. caraboides*'.

name, according to present practice, for the single *Cychrus* species of northern Europe. *Vide* also *Tenebrio rostratus*, below.

T. cursor, 1758 (p. 418; 1761, p. 225; 1767, p. 675). One specimen = *Oryzaephilus surinamensis* L., 1758 (p. 357, *Dermestes*; fam. Cucujidae), of which it is thus a synonym. The habitat given for *cursor*, "in Sueciae domibus" (1758, 1767), is in full accordance with this interpretation. The species is considered here only because Hope (1840, p. 53), in agreement with Fabricius (1801, p. 126, *Scarites*), suggested that *Tenebrio cursor* was a *Dyschirius*. The name was revived for *Lissodema cursor* (fam. Salpingidae) by Gyllenhal (1813, p. 716), who doubtfully identified it with the Linnaean species.

T. fossor, 1758 (p. 417; 1746, p. 177, no. 543, *Mordella*; 1761, p. 225; 1767, p. 675). One specimen = *Clivina fossor* auct. The descriptions are sufficient.

T. gibbus, 1761 (pp. 226-227; 1767, p. 676). No specimen in the London collection. In the 'Linnaean Collection' of Uppsala there is an exotic Tenebrionid under the name of "*Erodinus gibbus*", which does not fit the description at all. Hope (1840, p. 54) interpreted Linné's species as a *Zabrus*, probably influenced by Fabricius (1794, p. 442; 1801, p. 189) whose *Carabus gibbus* is *Zabrus tenebrioides* Gze., but Fabricius did not refer to Linné and the expression "nec punctatus aut sulcatus, etiam lateribus" (1761) seems to exclude any Carabid species. It should also be remarked that *Opatrum* (now: *Heliopathes* or *Phylan*) *gibbum* Fabricius (1775, p. 76) was described without reference to *Tenebrio gibbus* L. This remains uninterpreted.

T. rostratus, 1761 (p. 226; 1767, p. 667). One specimen, labelled "*Rostratus*" (in Linné's hand) = *Cychrus caraboides* L., auct., with dull, pronouncedly granulate elytra and narrow prothorax, which has the sides faintly sinuate basally, thus belonging to the race of the plain and of more southern regions, i.e. the subsp. *rostratus* auct. The description ("thorax Carabi, valde angustus & Caput angustissimum", etc.) figures a *Cychrus* far better than does that of *Tenebrio caraboides*. It seems remarkable that Linné should have described a so characteristic species twice but the explanation suggested by Roeschke (1907, pp. 217-220) that Linné in 1761 probably had no specimen of the earlier described *Caraboides* at hand, may be correct. Though nothing supports Roeschke's opinion (*l. c.*, p. 220) that *caraboides* and *rostratus* refer respectively to the two main races of the species, I think it most convenient to retain this practice in future nomenclature.

CONCLUSIONS.

1. PROPOSED CHANGES IN USE OF SOME LINNAEAN NAMES.

Carabus caeruleus auct. (nec Linné, 1758) should be replaced by *Pterostichus* (*Poecilus*) *versicolor* Sturm, 1824.

Carabus ustulatus auct. (nec Linné, 1758) should be replaced by *Bembidion* (*Peryphus*) *tetracolum* Say, 1823.

Carabus vulgaris Linné, 1758 cannot be used for *Amara* (s. str.) *lunicollis* Schioedte, 1837, nor for any other *Amara*, nor for *Pterostichus* (*Omasus*) *melanarius* Illiger, 1798.

Cicindela rupestris auct. (nec Linné, 1767) should be replaced by *Bembidion* (*Peryphus*) *bruxellense* Wesmål, 1835.

It is proposed that these four Linnaean species' names should be altogether abandoned: (i) they cannot be interpreted with certainty, and (ii) their transmission to another, related species would lead to irreparable confusion.

2. LINNAEAN NAMES WHICH CANNOT BE INTERPRETED.

Carabus buprestoides, 1767.

Carabus spinipes, 1758.

Carabus testaceus, 1761.

3. LINNAEAN SPECIES DESCRIBED AS CARABUS BUT NOT BELONGING TO THE CARABIDÆ.

Carabus quadripustulatus, 1761.4. LINNAEAN SPECIES DESCRIBED UNDER ATTELABUS OR TENEBRIO
BUT BELONGING TO THE CARABIDÆ.*Attelabus melanurus*, 1767.*A. pensylvanicus*, 1767.*A. surinamensis*, 1767.*Tenebrio caraboides*, 1758 (*rostratus*, 1761).*T. fossor*, 1758.5. THE PRESENT STATE OF THE VALID LINNAEAN SPECIES OF CARABIDÆ,
56 IN NUMBER, ARRANGED IN ALPHABETICAL ORDER.

<i>Acupalpus meridianus</i> , 1761 (Carabus)	Terra typica
<i>Agonum marginatum</i> , 1758 (Carabus)	Suecia
<i>A. (Europhilus) piceum</i> , 1758 (Carabus)	Suecia
<i>A. sexpunctatum</i> , 1758 (Carabus)	Suecia
	(Uppsala)
<i>Asaphidion flavipes</i> , 1761 (Cicindela)	Suecia
<i>Bembidion (Testedium) bipunctatum</i> , 1761 (Carabus)	Suecia
<i>B. (s. str.) quadrimaculatum</i> , 1761 (Cicindela)	Suecia
<i>B. (Chrysobraceon) velox</i> , 1761 (Carabus)	Suecia
	(Ins. Fårö)
<i>Blethisa multipunctata</i> , 1758 (Carabus)	Suecia
<i>Brachynus crepitans</i> , 1758 (Carabus)	Suecia
<i>Broscus cephalotes</i> , 1758 (Carabus)	Suecia
<i>Calathus melanocephalus</i> , 1758 (Carabus)	Suecia
<i>Calosoma inquisitor</i> , 1758 (Carabus)	Suecia
<i>C. sycophanta</i> , 1758 (Carabus)	Suecia ?
<i>Carabus auratus</i> , 1761	Suecia ?
<i>C. clathratus</i> , 1761	Suecia
<i>C. (Procrustes) coriaceus</i> , 1758	Germania
<i>C. granulatus</i> , 1758	Suecia
<i>C. hortensis</i> , 1758	Suecia
<i>C. intricatus</i> , 1761	Germania
<i>C. nitens</i> , 1758	Suecia
<i>C. violaceus</i> , 1758	Suecia
<i>Cicindela campestris</i> , 1758	Suecia
<i>C. capensis</i> , 1764	Cape Colony
<i>C. germanica</i> , 1758	Germania
<i>C. hybrida</i> , 1758	Suecia
<i>C. maura</i> , 1758	Algeria
<i>C. sylvatica</i> , 1758	Suecia
<i>Clivina fossor</i> , 1758 (Tenebrio)	Suecia
<i>Colliuris (Odacanthella, Casnonia) pensylvanica</i> , 1767 (Attelabus)	U.S.A.
<i>C. surinamensis</i> , 1767 (Attelabus)	Surinam
<i>Cychrus caraboides</i> , 1758 (<i>rostratus</i> , 1761) (Tenebrio)	Suecia
<i>Cymindis vaporariorum</i> , 1758 (Carabus)	Suecia
	(Uppsala)
<i>Demetrias atricapillus</i> , 1758 (Carabus)	Germania
<i>Diachromus germanus</i> , 1758 (Carabus)	Germania
<i>Dromius quadrimaculatus</i> , 1758 (Carabus)	Suecia
<i>Elaphrus riparius</i> , 1758 (Cicindela)	Suecia
<i>Eurynebria complanata</i> , 1767 (Carabus)	Hispania

<i>Galerita americana</i> , 1758 (Carabus)	Surinam
<i>Harpalus latus</i> , 1758 (Carabus)	Suecia
<i>Lebia crux-minor</i> , 1758 (Carabus)	Suecia
<i>L. cyanocephala</i> , 1758 (Carabus)	Suecia
<i>Leistus ferrugineus</i> , 1758 (Carabus)	Suecia
<i>Megacephala (Tetracha) carolina</i> , 1763 (Cicindela)	U.S.A.
<i>M. (T.) virginica</i> , 1767 (Cicindela)	U.S.A.
<i>Metabletus truncatellus</i> , 1761 (Carabus)	Suecia
<i>Nebria livida</i> , 1758 (Carabus)	Suecia
<i>Notiophilus aquaticus</i> , 1758 (Cicindela)	Suecia
<i>Odacantha melanura</i> , 1767 (Attelabus)	Suecia
	(Uppsala)
<i>Panagaeus crux-major</i> , 1758 (Carabus)	Suecia
<i>Pheropsophus aequinoctialis</i> , 1763 (Cicindela)	Surinam
<i>Ph. bimaculatus</i> , 1771 (Carabus)	India ?
<i>Ph. fastigiatus</i> , 1764 (Carabus)	Cape Colony
<i>Pterostichus (Poecilus) cupreus</i> , 1758 (Carabus)	Suecia
<i>Sphodrus leucophthalmus</i> , 1758 (Carabus)	Suecia
<i>Thermophilum decemguttatum</i> , 1764 (Carabus)	Cape Colony

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THE MARINE HEMIPTERA OF THE MONTE BELLO ISLANDS, WITH
 DESCRIPTIONS OF SOME ALLIED SPECIES. By W. E. CHINA, M.A., Sc.D.
 (Communicated by Dr. A. T. HOPWOOD F.L.S.)

(With text-figures 1-6.)

[Read 19th January 1956.]

INTRODUCTION.

Our knowledge to date of the Hemiptera of the Monte Bello Islands can be summed up in the following quotation from P. D. Montague's paper (1914): "Of other insects the Hemiptera were not well represented, the majority of forms being Homoptera. Two species of water bugs were obtained from the Home Lagoon, Hermite, one closely resembling *Hermatobatodes marcheï* Coutière et Martin and the other *Halobates wüllerstorffi* (Frauenf.); both appear to have points of specific difference".

Unfortunately this material, unlike that comprising the Lepidoptera and some Diptera, did not reach the British Museum (Nat. Hist.) and has apparently been lost. The species near *Hermatobatodes marcheï* Coutière et Martin (1901) was probably the species described below as *Hermatobates weddi*, sp. nov., which was recently taken in the Islands by Surgeon Commander Wedd, R.N., while the *Halobates wüllerstorffi* of Montague was probably *Halobates regalis* Carp. (1892) which was also collected by the Commander. Altogether the Campania collectors obtained 16 species of Heteroptera and 7 species of Homoptera which have already been listed in Appendix 2 of Dr. F. L. Hill's paper* (Hill, 1955). It is not proposed to describe the new species of common Australian genera which can best be dealt with in monographs of the genera in question, but the marine Heteroptera are of special interest and are listed or described as follows.

Family **Gerridae**.

Subfamily *HALOBATINAE*.

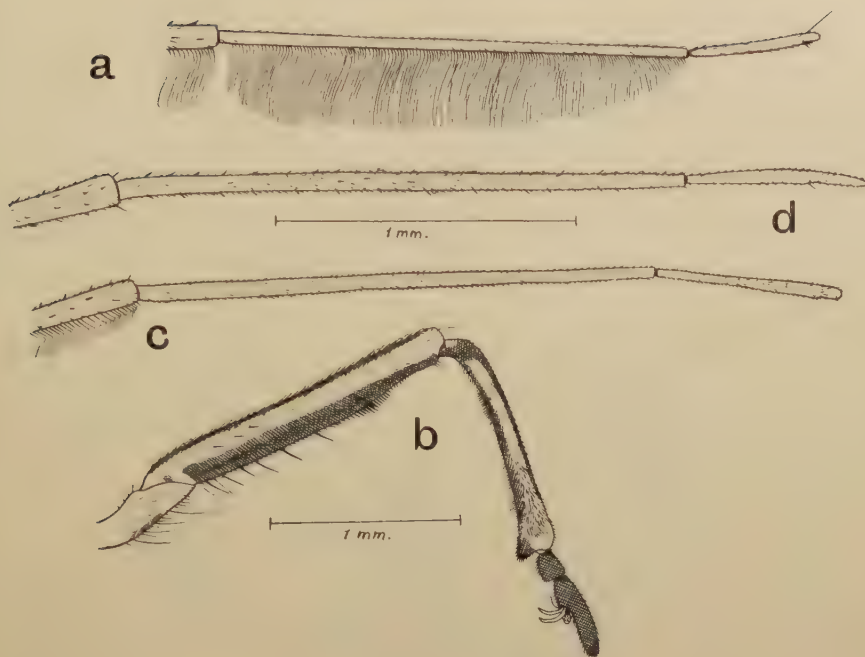
Halobates (*Hilliella*, subg. n.) *mjobergi* Hale. (Figs. 1, 2, 3.)

Halobates mjobergi Hale, 1925, *Arkiv. för Zoologi*, **17A**, 20 : 12-14.

Habitat: South Hermite, 2 males, 3 females and 1 nymph from Mangrove swamp, 25. viii. 1952 (F. L. Hill).

This species was first collected at Broome, on the west coast of Australia, about 470 miles north west of the Monte Bello Islands, by Dr. E. Mjoberg during the Swedish Scientific Expedition to Australia from 1910 to 1913. Mjoberg found it jumping on the surface of the salt-water lagoons amongst mangrove roots, during ebb-tide. Some were even taken in copula on flowers, presumably of emergent vegetation. Others were taken in copula on salt water amongst mangrove swamps at low water. One of Mjoberg's labels reads "Lives on salt water, sand and mangrove vegetation". Dr. Hill also collected his specimens from mangrove swamps on the southern shore of Hermite, probably in the Home Lagoon mentioned by Montague. Hale pointed out that in *H. mjobergi* the hairs fringing the intermediate tibiae and tarsi are short, a feature which Buchanan White (1883), thought might be characteristic of species living near the shore. Actually the normal fringe of swimming hairs on the first tarsal segment of the middle leg (fig. 1c) is completely absent in *Halobates mjobergi*, such short hairs as are present being merely ordinary pubescence. *H. mjobergi* Hale (1925) is closely allied to the S. Formosan *H. apicalis* Esaki (1924). Esaki (1926) has shown that *H. mjobergi* Hale, *H. apicalis* Esaki and *H. shiranui*

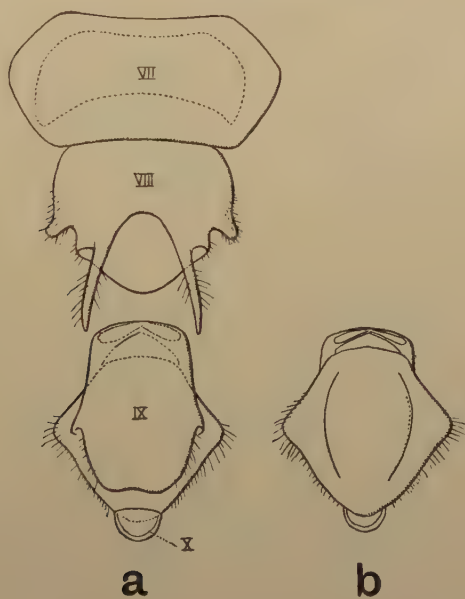
* It is necessary here to correct a serious error which crept into the list of Hemiptera published in Appendix 2, p. 120. The last item should read Eurybrachyidae gen. et sp. nov.—not "Tettigometridae gen. et sp. nov."

FIG. 1.—*Halobates sewelli* Imms.

a, Tarsus of middle leg to show swimming hairs.

Halobates (*Hilliella* subg. nov.) *mjobergi* Hale.

b, Front leg. c, Tarsus of middle leg, note absence of swimming hairs. d, Tarsus of hind leg.

FIG. 2.—*Halobates* (*Hilliella* subg. n.) *mjobergi* Hale ♂.

a, Ventral view of genital segments. b, Dorsal view of 9th abdominal tergite.

Esaki constitute a separate group distinguished by having the first anterior tarsal joint very short (fig. 1 *b*) and the blackish area of the head much reduced. I consider, however, that *H. apicalis* Esaki and *H. mjobergi* Hale are much more closely related agreeing not only in the short first anterior tarsus and distinctive armature of the anterior femur (fig. 1 *b*) but in the complete absence of the swimming fringe of hairs on the first tarsal segment of middle leg (fig. 1 *c*), in the very unusual pallid striping of the front and middle femora and tibiae and in the hairy processes of the 8th abdominal segment in the male (fig. 2 *a*). I therefore propose a new subgenus *Hilliella* to hold these two species, with type species *H. mjobergi* Hale. Both these species are associated with a sea-shore habitat rather than a fully marine

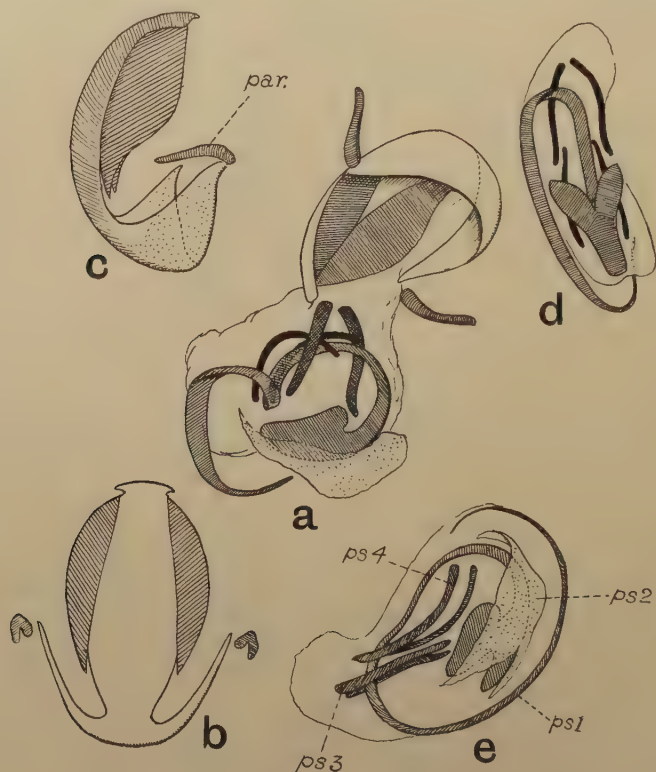


FIG. 3.—*Halobates* (*Hilliella* subg. nov.) *mjobergi* Hale ♂.

a, Aedeagus distended as in copula, showing the position taken up by the sclerotized pieces in the swell body. *b*, Lever (theca) from below showing parameres in end view. *c*, Lever (theca) in side view (only one paramere (*par.*) shown). *d*, Swell-body (at rest) in ventral view. *e*, Swell-body (at rest) in lateral view; *ps* 1, 2 & 3 the sclerotized pieces of Ekblom; *ps* 4 additional pair of sclerotized pieces not found in *Gerris asper*.

one. *H. shiranui* although possessing the short anterior first tarsal segment has the normal hair fringe present on the middle first tarsal segment and the femora are of normal uniform blue-black colour. The new subgenus is dedicated to Dr. F. L. Hill in recognition of the part he played in investigating the Monte Bello insects.

The internal structure of the male genitalia in *Halobates* has never been adequately studied. The only figure of the aedeagus in this genus was given by Imms (1936) but the structure was not properly understood and two sclerotized pieces in the swell-body were mistaken for parameres. It was, therefore, very satisfying to find

a male of *H. (Hilliella) mjobergi* Hale with distended aedeagus showing how this complicated apparatus works. This aedeagus has been fully figured (fig. 3). Unfortunately the ejaculatory duct was destroyed in the ordinary technique for preparation of sclerotized structures. The difference between the swell-body and its contents in the subgenera *Halobates* and *Hilliella* can be seen by comparing Imms' fig. 7 b with my fig. 3. Actually exactly the same number and type of sclerotized pieces are present in both subgenera (although not shown in Imms' figure) but the vesica in *Halobates* presents a hole in its middle and the distal extremity is long and filiform.

Halobates (Halobates) regalis Carpenter.

Halobates regalis Carpenter, 1892, *Proc. Roy. Dublin Soc.* (ns), **7**, 144.

Habitat: South Hermite, 8 males, 6 females and several nymphs, October 1952. (Surg.-Commr. G. Wedd, R.N.)

This species was described from the Torres Straits between Queensland and New Guinea, but has since been recorded from the Arafura Sea and Port Darwin (Hale, 1925). It belongs to the typical subgenus *Halobates*.

Subfamily HERMATOBATINAE. *

Hermatobates haddoni Carpenter. (Figs. 4 c, 5 a-c.)

Hermatobates haddoni Carpenter, 1891, *Proc. Roy. Dublin Soc.* (ns), **7**, 143, pl. XII, figs. 4-8.

Hermatobates haddoni Bergroth, 1906, *Wien. ent. Zeit.* **25**, 1-12; Esaki, 1947, *Mushi*, **18**, pt. 7, 49-51; China & Usinger, 1950, *Proc. Hawaiian Ent. Soc.* **14**, no. 1, 53.

Habitat: South Hermite, 1 male and 1 nymph, 23. x. 1952 (Surg.-Commr. G. Wedd, R.N.)

Esaki (1947) has given an account of the biology of *Hermatobates*. It inhabits coral reefs which are exposed only for a short time at low tide and is thus submerged twice each day to a depth of some ten feet. It appears to remain in crevices in the coral, in between the shells of dead bivalve molluscs (*Tridacna*) and under blocks of loose coral. At low tide the bugs appear on the surface of small tidal pools in the sunshine and glide about on the surface in quite a different way from that of other water-striders. They are able to climb and walk rapidly on the dry coral no doubt aided by the flexible three-segmented tarsi. When the tide begins to turn or the sun goes behind a cloud, the bugs quickly disappear from the surface of the water. *H. haddoni* is found in association with certain Collembola, halophilous midges of the genus *Clunio* and minute water-striders of the genus *Halovelis*. The Haloveliids, and probably the Hermatobatids also, feed on the midges and perhaps also on the Collembola.

Hermatobates haddoni has previously been recorded from: Mabuaig, Torres Straits (Haddon); Guichen Reef near Troughton Island, West Australia (Walker); Honda Bay, Palawan Philippine Islands (Marche); Ishigaki Island, Yaeyama Group, Ryunku Islands (Ikeda); New Caledonia (Esaki) and Tahuata, Marquesas Islands (Cheesman). Miss Cheesman's Marquesan specimen is a nymph. The unique type specimen described by Carpenter is a male. Females appear to be rare.

A closely related species *H. djiboutensis* Coutière et Martin (1901) has been described from the Red Sea.

Although Esaki (1947) has synonymized *Hermatobatodes marche* C. & M. (1901) from the Philippines with *Hermatobates haddoni* Carpenter from the Torres Straits, the former differs from the latter in possessing in the male a distinct 4th abdominal tergite in addition to the 5th, 6th and 7th abdominal tergites found in *H. djiboutensis* C. & M. and in *H. haddoni* Carp. The anterior femur in *H. haddoni* differs from

* For the proper study of the structure, specimens of Hermatobatinae and also of the Veliid subfamily Haloveliinae must be cleared, mounted on slides and examined under the high powered monocular microscope.

H. marchei in being much more swollen and in possessing only 7-8 small spines between the proximal and distal large spines instead of 12 as in *H. marchei*. The anterior tibia also possesses a tubercle on the outer side towards the apex which is absent in *H. marchei* and the hind femur is distinctly thickened on the basal third whereas in *H. marchei* the hind femur is more or less uniformly thick. I propose, therefore, to resurrect *H. marchei* C. & M. from synonymy under *H. haddoni* Carp. although retaining for the present the synonymy of *Hermatobatodes* under *Hermatobates*. Investigation of the material collected on Guichen Reef by Commander J. J. Walker in 1890, reveals the fact that only one male belongs to *H. haddoni* Carpenter : the remaining two represent a new species which is briefly described here although not forming part of the Monte Bello fauna.

Hermatobates walkeri, sp. nov. (Figs. 4 a, 5 g-i.)

Description : ♂ distinctly smaller and narrower than *H. haddoni* Carpenter but differing principally in the much less inflated anterior femora (fig. 5 h) and in the non-inflated posterior femora (fig. 5 i) : in this latter character resembling *H. marchei* C. & M.

Armature of anterior femur and tibia as in fig. 5 h, g. First antennal segment distinctly shorter than in *H. haddoni* being distinctly shorter than the second whereas in *H. haddoni* the first two segments are subequal. Relative lengths of segments 45 : 50 : 35 : 38 whereas in *H. haddoni* the lengths are 65 : 67 : 45 : 48 (68=1 mm.). Relative lengths of rostral segments 15 : 7 : 22 : 16.

Meso- and meta-sterna separated by a more or less distinct suture (fig. 4 a) which is absent in *H. haddoni* (fig. 4 c). Internal male genitalia (aedeagus) different in detailed structure from *H. haddoni*.

Differs from *H. marchei* C. & M. in smaller size, presence of only three visible abdominal tergites instead of four, smaller number of anterior femoral spines, in first antennal segment distinctly shorter than second and in the absence of the median lobe on posterior margin of metasternum.

Differs from *H. djiboutensis* C. & M. in the slender anterior femora with more spines and in the differently armed trochanters and tibiae.

H. walkeri is the smallest of the four species of *Hermatobates* measuring only 2.70 mm. in length, but size is not important as according to Professor Esaki considerable variation occurs in this respect. For detailed measurements see table under the description of the next species.

Habitat : North Western Australia, Arafura Sea, Guichen Reef near Troughton Island, J. J. Walker, 1890, 1 holotype and 1 paratype males (in Brit. Mus. (Nat. Hist.) collected in company with *H. haddoni* Carpenter (see Walker, J. J., *Ent. Mon. Mag.*, 1893, p. 229).

Hermatobates weddi, sp. nov. (Figs. 4 b, 5 d-f.)

Description : ♂ Colour : Dorsum bluish-black, matt, with fine silver-grey pubescence; reflexed pleural region blue-grey, matt with the minute abdominal spiracles shining black; head blue-gray, matt, basal margin blackish with a row of four large orange spots; first and second antennal segments infusate with basal third of the first segment pallid yellow, pubescence silver-grey; third and fourth segments missing in unique type specimen; rostrum infusate, apex black; eyes reddish black. Under-side of head and sternum blue-grey, matt, genital segments infusate shining; acetabulae pallid yellow, the anterior pair infusate on outer side; anterior coxae and trochanters sordid pale yellow; middle and hind coxae dark shining brown the latter somewhat pallid beneath; middle and hind trochanters shining brown on apical half, pallid on basal half; femora, tibiae and tarsi shining brown, the underside of the anterior femora and the apices of anterior tibiae rather more pallid.

♂ Structure : Head transverse, four times wider across eyes than long in middle; from above triangular with the apex truncate and the antenniferous tubercles prominent, lateral margins concave, posterior margin straight; eyes relatively small about one-quarter the width of vertex between eyes (18 : 70) which is nearly twice as wide as length of head seen from above (70 : 38); covered with short,

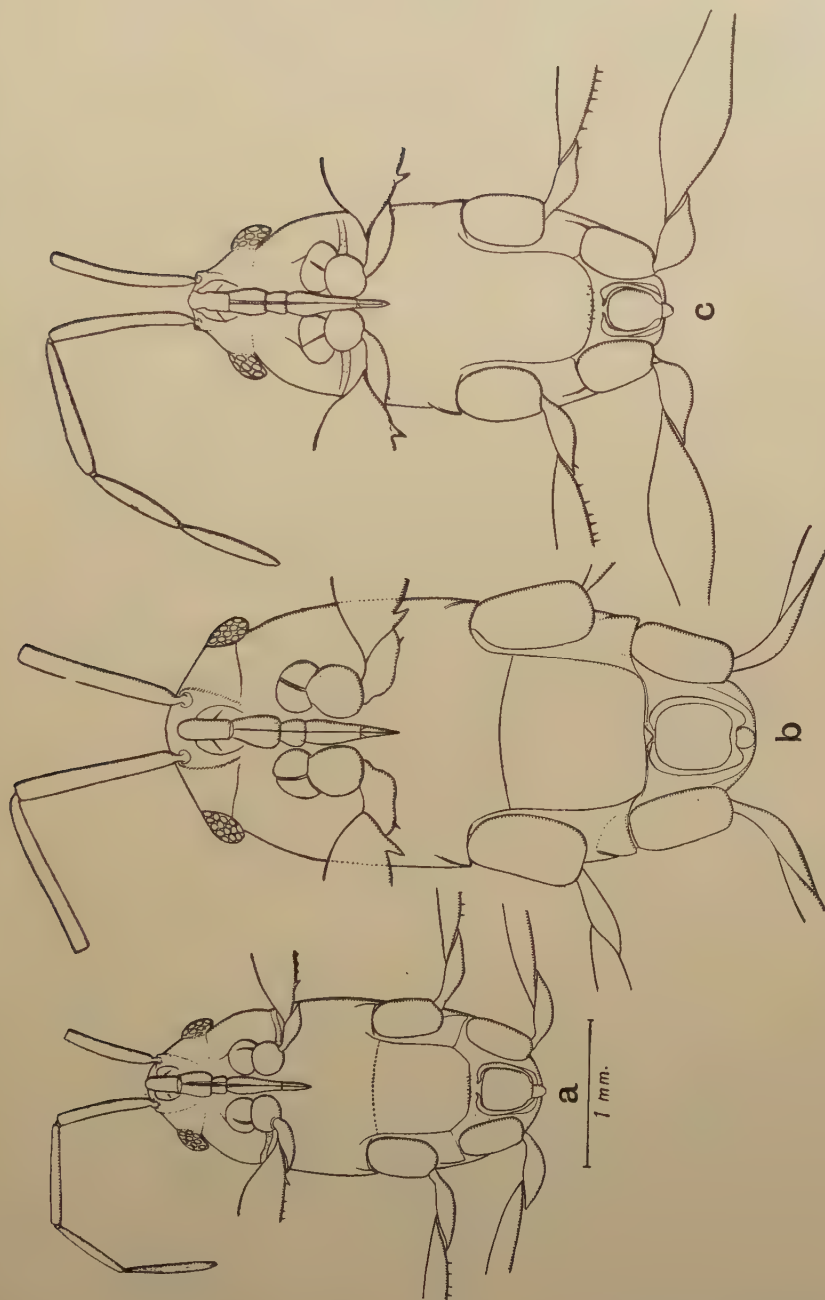


FIG. 4.—Ventral view of : *a*, *Hermatobates walkeri*, sp. nov., ♂, *b*, *Hermatobates veddai*, sp. nov., ♂, *c*, *Hermatobates haddonii* Carpenter, ♂. All to same scale.

erect, pale pubescence and with tufts of longer hairs at apex in middle and on each side: eyes with short erect bristles: a distinct fine suture running close to basal margin of head, broadly anteriorly sinuate in middle and narrowly sinuate on each side and apparently separating base of frons from vertex: clypeus prominent between antenniferous tubercles. Relative lengths of antennal segments one and two, 70:78 (other segments missing in the unique type specimen), these segments densely covered with erect pale hairs which are much longer on the first than on the

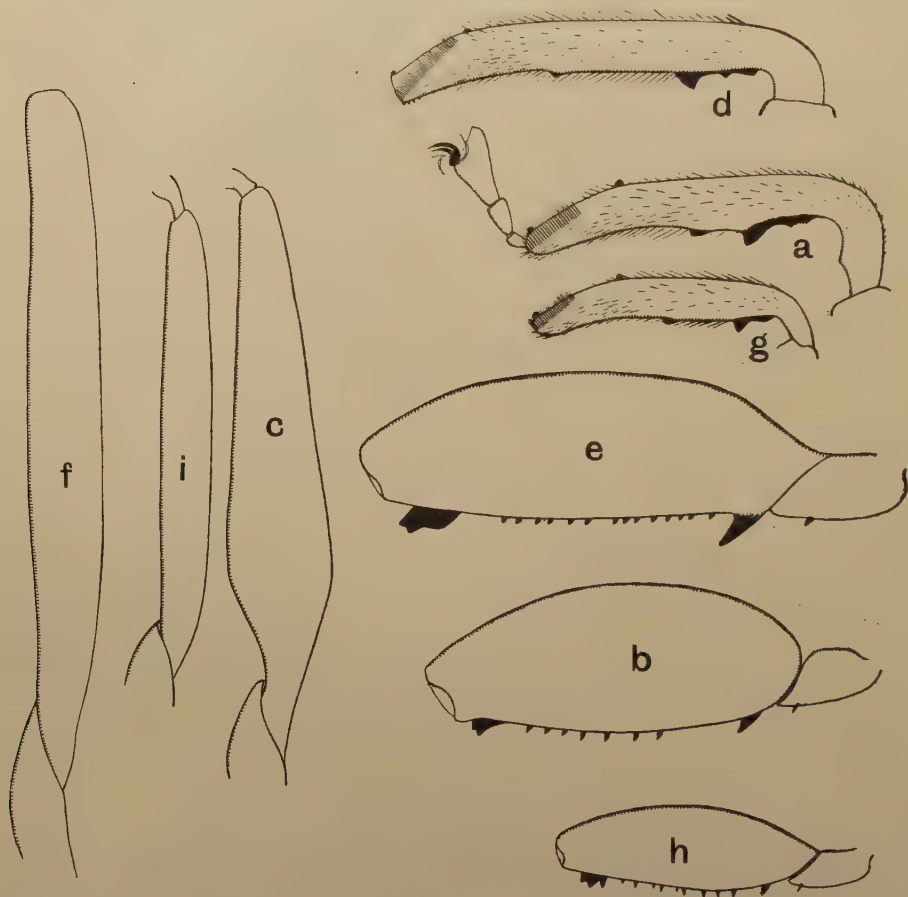


FIG. 5.—*Hermatobates haddoni* Carpenter, ♂.
a, Anterior tibia and tarsus. *b*, Anterior femur. *c*, Posterior femur.
Hermatobates weddi, sp. nov., ♂.
d, Anterior tibia. *e*, Anterior femur. *f*, Posterior femur.
Hermatobates walkeri, sp. nov., ♂.
g, Anterior tibia. *h*, Anterior femur. *i*, Posterior femur.
 All to same scale.

second. Rostrum extending a little beyond the bases of the anterior trochanters, relative lengths of segments: 25:10:21:20.

Pronotum very short, little more than half the width of an eye (9:16) widening to each side behind the eyes, pubescence very short and very fine. Fused mesonotum, metanotum and first to fourth abdominal segments matt with a fine short pubescence on disc, the hairs becoming much longer laterally and posteriorly: suture between

the meso- and meta-sterna distinct as in *H. walkeri*; posterior margin of meta-sternum in middle with a distinct triangular prominence as in *H. marchei* C. & M. Anterior trochanter with a single small tooth towards apex; anterior femur (fig. 5 e) strongly incrassate, the under side covered with long hairs with a strong moderately long apically black spur at base directed obliquely towards the apex, an apically bifid black tooth at the apex and between these 14 small teeth; anterior tibia (fig. 5 d) covered with long hairs which are erect on the outer side and directed towards apex of tibia on inner side, base of latter with a black thickening ending apically in a black tooth, a small tooth a little beyond the middle and several small black tubercles at the apex; apex of tibiae with the usual two oblique combs of bristles one on inner surface and one on outer surface, the latter longer than the other and ending basally in a black tubercle. Middle femur slightly thickened before the middle, densely covered with long hairs, the underside with about 20 distinct spines longer and hooked towards base and shorter and straight towards apex; trochanter with a short tooth towards apex, tibia and tarsus laterally compressed, with long pubescence, tarsi three-segmented; hind femur unarmed, only slightly thickened in middle, covered with long hairs; hind tibia and tarsus covered with long hairs, laterally compressed, the tarsus concave below and convex above.

First abdominal spiracles dorsal, placed laterally close to margin of fused anterior segment and in line with posterior third of middle coxae. Second to seventh abdominal spiracles all distinctly visible placed ventrally on reflexed pleural region as in *H. marchei* C. & M. Only the fourth, fifth and seventh dorsal abdominal segments visible, the sixth and seventh being fused; fourth segment indistinctly delimited in the middle but with median scent-gland scar.

Processes of the eighth segment figured (fig. 4 b) similar to those in the other species but differing in detail of the apices; ninth segment (genital capsule) hemispherical, much more prominent than in the other species.

Total length 4 mm., greatest width 1.9 mm.

Detailed measurements as in comparative table which follows; (43.5=1 mm.)

TABLE I.

	<i>H. haddoni</i> Carp. Type ♂			<i>H. walkeri</i> sp. nov. Type ♂			<i>H. weddi</i> sp. nov. Type ♂		
Body length	140			115			173		
Greatest width (ex. coxae)	68			53			83		
Length femur 1	70			44			80		
Width femur 1	26			12			26		
Length femur 2	89			65			108		
Length femur 3	90			70			113		
Length tibia 1	62			42			70		
Length tibia 2	62			44			64		
Length tibia 3	62			47			63		
Tarsus 1	2.5	5	12	2	5	9	2	5	15
Tarsus 2	5	26	—	4	20	14	4	31	27
Tarsus 3	5	22	21	3.5	20	18	5	27	27

Habitat: Monte Bello Islands, S. Hermite, on coral reef connecting mainland south coast with a small islet. 1 ♂ holotype in British Museum (Nat. Hist.) collected by Surgeon-Commander G. Wedd, R.N., October 1952.

Remarks: Closely allied to *H. marcheii* Cout. et Martin but differs in having more small teeth (14) on the anterior femur, in the presence of a tubercle on inner side of anterior tibia about two-thirds from base and four additional small tubercles close together at apex of inner side, in the presence of a suture between the meso- and metasterna (fig. 4 b) and in the three-segmented abdomen in dorsal view, 6 and 7 being fused. If Coutière and Martin's genus *Hermatobatodes* were to be regarded as distinct from *Hermatobates* Carpenter, *H. weddi* would be placed in that genus or subgenus. Both these species have the very transverse head and the posterior margin of metasternum in middle with a distinct prominence.

Key to species of Hermatobates.

1. Head four or more times as wide across eyes as in middle (fig. 4 b). Posterior margin of metasternum with a small median lobe or prominence in front of the genital segments and lying between the apices of the anteriorly directed processes of the eighth abdominal segment (fig. 4 b); no minute conical tubercles 2.
- Head much less transverse, about three times as wide as long. Posterior margin of metasternum straight or slightly emarginate, no median prominence, only a number of minute conical teeth (figs. 4 a & c) 3.
2. Fourteen small teeth on anterior femur between basal and apical spurs (fig. 5 e); anterior tibia with a small tubercle on inner side about two-thirds from base and four additional small tubercles close together at apex (fig. 5 d); suture between meso- and meta-sterna distinct (fig. 4 b); 6th abdominal tergite absent or fused with 7th. Monte Bello Is. *H. weddi*, sp. nov.
- Twelve small teeth on anterior femur between basal and apical spurs; anterior tibia without tubercles on the inner side of apical half; 6th abdominal segment distinctly delimited from 7th. Philippines *H. marcheii* Cout. & Martin.
3. Anterior femur strongly incrassate, little more than twice as long as wide (fig. 5 b); 1st antennal segment subequal to 2nd. 4.
- Anterior femur feebly incrassate (fig. 5 h), more than three times longer than wide; 1st antennal segment distinctly shorter than 2nd. Arafura Sea *H. walkeri*, sp. nov.
4. Posterior femur in male equally thick throughout; anterior trochanter with several (3) spines or teeth; anterior femur with six small teeth between basal and apical spurs; inner side of anterior tibia with three equidistant spurs. French Somaliland (Gulf of Aden) *H. djiboutensis* Cout. & Martin.
- Posterior femur in male with the basal third distinctly swollen (fig. 5 c); anterior trochanter with a single small spine (fig. 5 b); anterior femur with 7-8 small teeth between basal and apical spurs; inner side of anterior tibia with only two distinct teeth placed on basal half. Monte Bello Is., Arafura Sea, Torres Straits *H. haddoni* Carpenter.

Family Veliidae.

Subfamily HALOVELIINAE.

Halovelina Bergroth.

Bergroth E., 1893, *Ent. monthly Mag.* (2), 4, 277.

There has been some difference of opinion as to the family status of *Halovelina* and allied genera.

It was described by Bergroth (1893) as a Veliid but Esaki (1924 b) transferred it to the Gerridae on the basis of the four-jointed rostrum, the unusually long distance between the bases of the anterior and posterior legs and the long intermediate femora.

In 1926 Esaki (1926, p. 158) published a communication he had received from Bergroth to the effect that Bergroth, after a careful examination of the type specimens of *H. maritima* and *H. amphibia*, still considered that the genus belonged to the Veliidae. Esaki, however, refused to change his opinion and stated that the structure of the intermediate and posterior acetabulae and the large difference in length between the intermediate and posterior legs, were typically Gerrid characters.

Usinger later (1946) considered that Bergroth (1893) and Hale (1926) were correct in placing *Halovelina* in the Veliidae on account of the metathoracic scent gland openings which he stated opened laterally. Judging by general appearance *Halovelina* certainly looks like a Gerrid of the subfamily Halobatinae especially in the position and structure of the legs, with the middle and hind legs close together and rather widely separated from the front pair.

According to Hale (1926) the anterior tarsus in *Halovelina maritima* is three-segmented but Esaki (1926) was unable to see the small basal segment and, in fact, microscope slide preparations show that there are only two segments. But the segmentation of the anterior tarsus does not hold as a means of distinguishing the Veliidae from the Gerridae. It is true that the latter normally possess two-segmented tarsi but in the Veliidae the segmentation varies from one to three. Hale (1926) demonstrated the presence of a longitudinal comb at the apex of the anterior tibia in males of *Microvelia* and this is present in other genera of Veliidae (e.g. *Velia*). This character, however, which is present in *Halovelina*, is not constant being absent in some Veliid genera (e.g. *Veloidea* Gould and *Rhagovelina* Mayr) although it appears to be always absent in Gerridae. In some Veliids there is also a transversely oblique cleaning comb at the apex of the anterior tibia in both sexes which appears to be absent (except in *Hermatobates*) or very difficult to see in Gerridae.

The character of the three-segmented rostrum for separating Veliidae from four-segmented Gerridae, used by Hale (1926) is also valueless, the rostrum being four-segmented in both families.

In 1949 China and Usinger, in their key to the families of Gerroidea, separated Veliidae from Gerridae on the short middle femora and the presence of a median longitudinal groove on the vertex, absent in Gerridae. The latter character, has unfortunately been found to be unstable. In some Veliidae (e.g. *Microvelia* species and *Halovelina*) it is absent or obsolescent while in some Gerridae (*Rhagadotarsus* and *Rheumatobates*) it is present, so that the character cannot be used.

Nor can the presence of a lateral channel to the metathoracic scent gland, with its tufted apex above the hind acetabulum, be used to distinguish Veliidae from Gerridae since these channels are present in the otherwise typical Gerrid genera *Brachymetra*, *Cylindrostethus* and *Limnometra* and absent in *Halovelina*.

We are left therefore with the structure of the male genitalia. These are very complicated in the Gerroidea. According to Pruthi (1925) the two families scarcely merit separation on the basis of the male genitalia. Nevertheless in the Veliidae the parameres are large and distinct and visible in external view whereas in the Gerridae they are rudimentary and only visible on dissection. The so-called swell-body contained within the theca (basal plates of Pruthi) possesses two pairs of sclerotized pieces in both families but in the Gerridae there is also a long central piece (the ps. 1 of Ekblom, 1926) which is widened at the base and tapers to a point at the apex. Fortunately amongst the Monte Bello material were males of both *Halobates mjobergi* and *Halovelina hilli*, sp. nov., which had the aedeagus fully distended so that the parts could be studied in their functional positions. These are shown in figs. 3 and 6g. In the Gerrid (*Halobates*) the rudimentary parameres are seen attached to the base of the theca (basal plates) whilst in the Veliid (*Halovelina*) they are very long and distinct and articulated into the 9th segment in the usual way. In the Gerrid the long sclerotized median piece (vesica) of the swell-body (aedeagus) is distinctly seen attached to the apex of the membranous conjunctiva which arises from the basal plates, represented by the so-called theca. The two pairs of sclerotized strip-like pieces act as distenders of the inflated endosoma so

that the vesica (Ekblom's ps. 1) is free to move forward. Draped over the enlarged base of this vesica is an irregular laminate sclerite (Ekblom's ps. 2) of no known function but always present in Gerridae.

In the Veliidae the vesica is membranous so that Ekblom's sclerite ps. 1 with its associated sclerite ps. 2, are absent and only the two pairs of strip-like distensor sclerites are present.

The couplet 4 in China and Useringer's (1949, p. 50) key to the families of Gerroidea must therefore be modified as follows :—

4. Legs more or less equidistant (except in Haloveliinae and in *Husseyella* Herring, 1955 (Microveliinae)). Vertex usually with a distinct percurrent, median longitudinal suture or glabrous line, rarely obsolete or difficult to see (e.g. some species of *Microvelia*, *Halovelia*) in which case the eyes are relatively small, not extending backwards on to sides of pronotum. Scent gland usually with paired lateral channels terminating above hind acetabulae (except in *Halovelia*). Inner margin of eyes straight. Parameres large and distinct. Vesica of aedeagus membranous. Veliidae.
- Front legs widely separated from middle and hind pair. Vertex usually without a distinct percurrent, median longitudinal glabrous line or suture, such a suture rarely present (e.g. *Rhagadotarsus*, *Rheumatobates*) in which case eyes large, distinctly extending backwards on to sides of pronotum. Scent gland (omphalium) medial without lateral channels (except in *Brachymetra* *Limnometra* spp. and *Cylindrostethus*). Inner margin of eyes sinuate except in *Brachymetra*, the Halobatinae and the Rhagadotarsinae. Parameres rudimentary not visible without dissection. Vesica of aedeagus sclerotized forming the ps 1 sclerite of Ekblom, 1926. Gerridae.

According to Useringer (1946) the lateral scent channels typical of Veliidae are present in *Halovelia* but I am unable to verify this statement. In fact the metasternal scent gland opening is a median omphalium typical of the Gerridae. The intermediate nature of the Haloveliinae between the more specialized Gerridae and the more generalized Veliidae is of particular interest to the phylogenist and probably indicates that this subfamily lies at the base of the Gerridae in their evolution from the more primitive Veliidae. In the non-sinuate inner-margin of the eyes the Halobatinae and Rhagadotarsinae resemble the Veliidae and must therefore also lie at the base of the evolutionary development of the Gerridae. The structure of the male genitalia prevents these subfamilies from being united with the Haloveliinae to form a new family intermediate between the Veliidae and the Gerridae. *Cylindrostethus* which agrees with *Brachymetra* in possessing lateral scent-gland channels of the Veliid type possesses eyes of the Gerrid type and thus represents an early form of Gerridae subsequent to the development of the above subfamilies.

In studying the Monte Bello specimens of *Halovelia* it was at first thought that they represented *Halovelia septentrionalis* Esaki, a Japanese species but an analysis of the characters on which the known species are based and an examination of paratype material of this species very kindly sent to me by Professor Esaki showed that the Monte Bello species could be separated satisfactorily from *H. septentrionalis* Esaki, especially in the shorter intermediate legs and the shape of the male parameres.

Halovelia hilli, sp. nov.* (Fig. 6 e-h.)

Description : Colour ♂ and ♀: Velvety black with a greyish pubescence longer, denser and more distinctly grey in the male; base of vertex between the eyes with a median obscure dark ferrugineous spot, legs and antennae dark brownish-black.

Structure ♀: Body fusiform in female, the thorax strongly convex dorsally, the abdomen concave dorsally with only five visible segments; connexivum broad, reflexed with sutures obsolete except between the fourth and fifth visible abdominal segments; underside convex but with disc somewhat flattened, metasternum distinctly sutured off from mesosternum with a small scent-gland pore (omphalium) in middle of basal margin of mesosternum; abdomen with five visible ventral segments the apical (visible fifth) twice as long as the others, the basal four with a fine percurrent

* Dedicated to Dr. F. L. Hill in recognition of his work in collecting insects during his stay in the Monte Bello Islands.

median carina. Head about as long as wide between eyes (30 : 28)† : nearly three times as long as pronotum (30 : 11) : eye about one-quarter the width of vertex between eyes (7 : 28). Relative lengths of antennal segments 25 : 15 : 17 : 20, the first segment curved, the fourth fusiform : the first surpassing apex of head by two-thirds its length. Pronotum about one-third the length of head with its posterior margin straight, the suture obsolete in middle. Middle femur, much shorter than body, about as long as greatest width of thorax (76 : 75). Hind femur less than one-seventh as wide as its length (6 : 45) and slightly longer than hind tibia (45 : 43).

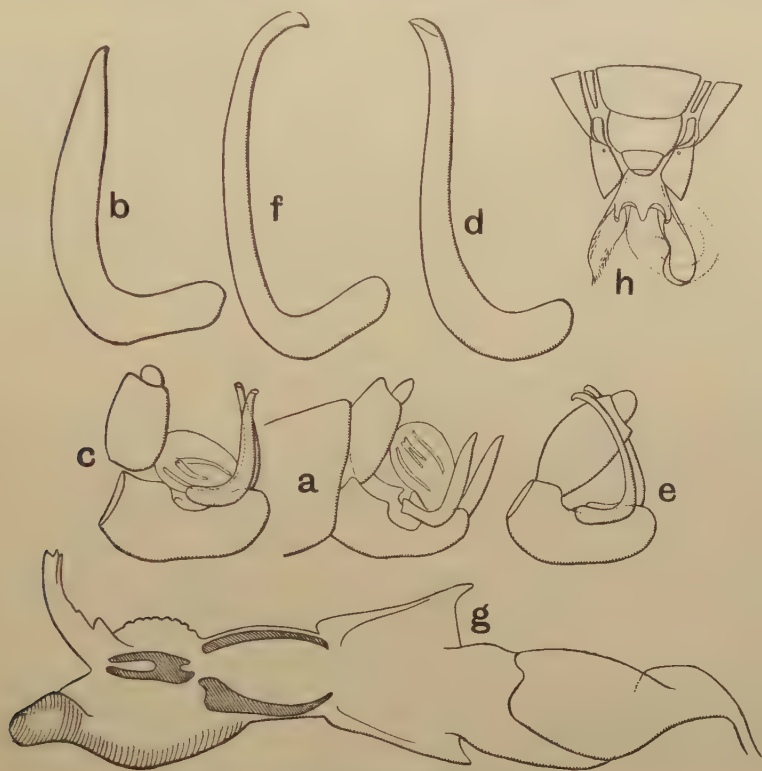


FIG. 6.—*Halovelgia maritima* Bergroth, ♂.

a, Lateral view of genitalia. b, Lateral view of paramere.

Halovelgia septentrionalis Esaki, ♂.

c, Lateral view of genitalia (note crossing of parameres). d, Lateral view of paramere.

Halovelgia hilli, sp. nov.

e, Lateral view of male genitalia (with theca and swell-body omitted). f, Lateral view of male paramere. g, Male aedeagus (swell-body) distended (as in copula). h, Dorsal view of female genitalia distended (as in copula).

Genitalia figured (fig. 6 h).

Length 2.07 mm. Greatest width across thorax 1.0 mm.

Structure ♂: Body shortly oval, the thorax and abdomen both moderately convex dorsally and flattened ventrally, pubescence distinctly more dense and relatively longer than in female: connexivum dorsally rounded, not reflexed, with three distinct sutures and only four visible segments excluding the eighth and ninth genital segments. Metasternum distinctly sutured off from mesosternum with scent-pore (omphalium) present in middle of basal margin of mesosternum. Head as long

† 70 = 1 mm.

as wide between eyes (25 : 25), eye rather less than one-quarter the width of vertex between eyes (7 : 25). Relative lengths of antennal segments 21 : 14 : 14 : 19.5. For relative lengths of legs in male see Table II following. Anterior apical tibial comb less than half length of tibia (3 : 8). Genitalia figured (fig. 6 *e-g*). Parameres long and slender with the apices distinctly curved inwards. Aedeagus shown fully extended in fig. 6 *g*.

Length 1.5 mm. Greatest width across thorax 0.85 mm.

Habitat : South Hermite, 1 ♂ type and 10 ♂ and 8 ♀ paratypes, mangrove swamp, August 1952, Surgeon-Commander G. Wedd, R.N. : 8 ♂ and 10 ♀ paratypes. Dr. F. L. Hill, 21. x. 1952 (several pairs in copula).

Type and paratypes in Brit. Mus. (Nat. Hist.).

Remarks : Closely allied to *H. septentrionalis* Esaki from Japan, the Loochoo Islands and Formosa but differs in having the second antennal segment slightly shorter than the third in both sexes, in the rostrum extending distinctly beyond the anterior coxae especially in the male and having the posterior femur less than two-thirds the length of the intermediate one. Parameres in male (fig. 6 *e*) not crossed as they are in *H. septentrionalis* Esaki (fig. 6 *c*) but directed anteriorly apically. The male genitalia of *H. maritima* Bergr. are figured (fig. 6 *a*) for comparison with those of *H. hilli*, sp. nov., and *H. septentrionalis* Esaki.

The following new species is described here for convenience although not forming part of the Monte Bello fauna.

Halovelis loyaltiensis, sp. nov.

Description : Colour ♂ and ♀ : Black with short more or less golden pubescence, mainly suberect but depressed to form definite spots on the mesonotum (one median and two lateral in male and two median and two lateral in female), and with long, depressed, silvery hairs forming silvery spots on abdomen, two in the female at basal angles of dorsum and three in male, in which there is an additional silvery area at apex of dorsum. These spots are only visible with the light at an angle (viewed posteriorly). Head with a pair of elongated fulvous spots one on each side of middle line at level of anterior margin of eyes, very distinct in female but obscure in male. There is also an obscure transverse fulvous band across base of head. Rostrum dark fulvous, tip black. Antennae and legs blackish brown with the extreme bases of first antennal segment fulvous and the trochanters all white. Underside of head, a transverse band across basal half of pronotum and some markings on underside of thorax and abdomen, fulvous. The fulvous markings much less distinct or obsolete in the male.

Structure ♂ : Head longer than wide between eyes (22 : 15) ; eyes relatively large, one-third the width of vertex between eyes (5 : 15) ; relative lengths of antennal segments 14 : 12 : 16 : 16 ; rostrum extending to anterior coxae. Pronotum about one-third the length of head (7 : 22), its posterior margin straight and the suture behind it well defined. Abdominal connexiva broad of equal width throughout, feebly reflexed, the whole dorsal surface feebly convex. Anterior and posterior femora strongly incrassate, anterior tibial comb short less than one-quarter total length of tibia (5 : 23) ; relative lengths of legs shown in Table II. Paramere long and slender as in *H. hilli* but distinctly shorter and without the apical inwards curve found in that species.

Total length 1.8 mm. Greatest width across the mesonotum 0.86 mm.

Structure ♀ : Differs from male in large size, strongly convex thorax and flattened abdominal dorsum within the reflexed connexiva, in the non-incrassate anterior and posterior femora and in the absence of anterior tibial comb. Relative lengths of antennal segments 16 : 14 : 19 : 19 ; rostrum extending to anterior trochanters. Relative lengths of legs : ant. femur 35, ant. tibia 28, tarsus 3 : 8 ; int. femur 75, int. tibia 71, int. tarsus 26 : 15 ; post. femur 44, post. tibia 42, post. tarsus 4 : 13. (43.5=1 mm.)

TABLE II.

Table of measurements of male *Halovelia* species represented in the British Museum (Nat. Hist.).

43·5 divisions=1 mm.

	<i>H. papuensis</i> Esaki. Paratype ♂.	<i>H. maritima</i> Berggr. Type ♂.	<i>H. malaya</i> Esaki. Type ♂.	<i>H. hilli</i> , sp. nov. Type ♂.	<i>H. loyaltiensis</i> , sp. nov. Type ♂.	<i>H. septentrionalis</i> Esaki. Paratype ♂.
Body length	77	84	83	66	82	72
Greatest width	35	45	43	35	39	45
Length femur 1	27	25	30	20	25	24
Length femur 2	82	37	60	41	57	48
Length femur 3	43	26	34	24	33	25
Length tibia 1	25	23	22	20	24	19
Length tibia 2	67	33	56	40	53	42
Length tibia 3	37	25	25	22	30	22
Tarsus 1	3 : 7	3 : 6	2 : 9	2 : 5	3 : 8	2 : 7
Tarsus 2	30 : 21	12 : 8	24 : 185	17 : 12	19 : 13	18 : 12
Tarsus 3	8 : 5	65 : 8	5 : 8	4 : 6	4 : 8	4 : 7
Antenna 1	17	11	20	14	14	14
Antenna 2	12	11	11	8	12	10
Antenna 3	13 : 5	14	12	9	16	10
Antenna 4	16	18	15	11	16	13 : 5

Hairs of cephalic trichobothria long, second antennal segment with a long bristle directed towards middle line at base of inner side.

Total length 2·4 mm. Greatest width across mesonotum 1·22 mm.

Habitat : Loyalty Islands, Faiaoye Bay, Uvea (Salt Lake). 1 ♂ type on (slide), 1 ♂ and 2 ♀ paratypes, 23. iii. 1953, M. Laird Coll. Type in Brit. Mus. (Nat. Hist.).

Remarks : Differs from all other species in the incrassate anterior and posterior femora in male and in distinctive pubescence forming silvery spots. Resembles *H. papuensis* and *H. marianarum* in long narrow head. Although the eyes are large they are proportionately much smaller than in *Entomovelina*.

The following key will, it is hoped, enable students to identify species in the genus *Halovelia*.

Key to species of the genus Halovelvia.

1. Head distinctly longer than wide between eyes* (at least 9 : 7) 2.
- Head not distinctly longer than wide between eyes (at most 11 : 10) 4.
2. Middle legs very long, the middle femur slightly longer than total length of head and body† together in male and longer than body alone in female ; eyes about half as wide as vertex between the eyes..... *H. papuensis* Esaki, New Guinea, Malaya.
- Middle femur not longer than total length of body alone, even in the male 3.
3. Eyes larger so that vertex between the eyes is $2^{1/3}$ times the width of one eye (14 : 6) ; 3rd antennal segment longer than 2nd (16 : 12) ; posterior margin of pronotum straight in middle ; front and hind femora distinctly thickened, the hind femur in middle wider than one quarter its length (8 : 25)..... *H. loyaltiensis*, sp. nov., Loyalty Islands.
- Eyes smaller so that vertex between eyes is $3^{5/7}$ width of one eye (13 : 3.5) ; 3rd antennal segment equal in length to 2nd ; posterior margin of pronotum sinuate in middle ; front and hind femora slender, the hind femur in middle not wider than one-sixth its length *H. marianarum* Usinger, Marianne Islands.
4. Second and third antennal segments subequal 7.
- Second antennal segment distinctly shorter than third 5.
5. Pronotum longer, the head twice as long as pronotum. First antennal segment surpassing apex of head by two-thirds its length *H. amphibia* Bergroth, Zanzibar.
- Pronotum shorter, the head about three times as long as pronotum. First antennal segment surpassing apex of head by only half its length 6.
6. Paramere long and slender, apical two-thirds cylindrical with apex distinctly curved inwards (fig. 6 f) *H. hilli*, sp. nov. Monte Bello Islands.
- Paramere shorter and broader, narrowing towards apex but not curved inwards at tip (fig. 6 b)..... *H. maritima* Bergroth, Cartier Islands.
7. Intermediate tibia and tarsus together longer than head and body together 8.
- Intermediate tibia and tarsus subequal to thorax and abdomen in males and shorter in female..... *septentrionalis* Esaki, Japan, Formosa.
8. Hind tibia nearly as long as femur *H. bergrothi* Esaki, New Guinea.
- Hind tibia much shorter than femur (25 : 34) *H. malaya* Esaki, Malaya.

* Esaki (1926) in his key to the species of *Halovelvia* couplet 1 (2), writes in error "between" whereas he meant "across".

† Body=thorax and abdomen together but does not include the head.

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THE SALTATORIAL ORTHOPTERA OF SOCOTRA.

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(With Plate 8, 38 Text-figures and 1 map.)

[Read 24 May, 1957.]

The island of Socotra has attracted several collecting expeditions and their results indicate that its fauna includes a very considerable proportion of endemic species and even genera. However, as regards Orthoptera in particular, the collections made there have been only incidental and no specialist in this group of insects visited the island until 1953, when the junior author had an opportunity to spend a few weeks on the island, in connection with locust control operations. The latter demanded a great deal of attention and only limited time could be devoted to collecting insects. Moreover, the season was not very favourable, as many Orthoptera were present only as young nymphs and there is little doubt that many even of the commoner species have, therefore, escaped notice. Nevertheless, all the previously recorded species were found as well as a surprisingly high number of new ones. It appeared, therefore, opportune to present a list of the Saltatorial Orthoptera of Socotra, including those recorded previously, although it is beyond doubt that the list is still far from being complete.

The taxonomic work on the present collection was divided between the two authors, G. B. Popov working out all Acrididae and Eumastacidae and B. P. Uvarov the remaining groups. The types and other specimens are in the British Museum (Natural History). Observations on the habitats and habits are, of course by G. B. Popov, while the zoogeographical discussion is by B. P. Uvarov.

The existing literature on the Orthopterous fauna of Socotra is restricted to six publications as follows:

- TASCHENBERG, O. 1883. Beiträge zur Fauna der Insel Socotra. *Z. Naturw.*, **56**, 184–185.
BURR, M. 1898. Orthoptera in: On a collection of Insects and Arachnids made by E. N. Bennet in Socotra. *Proc. Zool. Soc. Lond.*, 1898, 384–385.
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———. 1903. Earwigs, crickets and grasshoppers, in: *The Natural History of Socotra and Abd-el-Kuri*, 411–425, pl. XXV.
KRAUSS, H. A. 1902. Diagnosen neuer Orthopteren aus Südarabien und von der Insel Sokotra. *Anz. Akad. Wiss. Wien*, 1902, 1–5.
———. 1907. Orthopteren aus Südarabien und von der Insel Sokotra. *Denksch. Akad. Wiss. Wien*, mat. nat. Kl., **71**, 1–30, 2 pl.

To avoid repetition, these papers will be quoted in the list below by the author's names and the dates.

LIST OF SPECIES.

Family GRYLLACRIDIDAE.

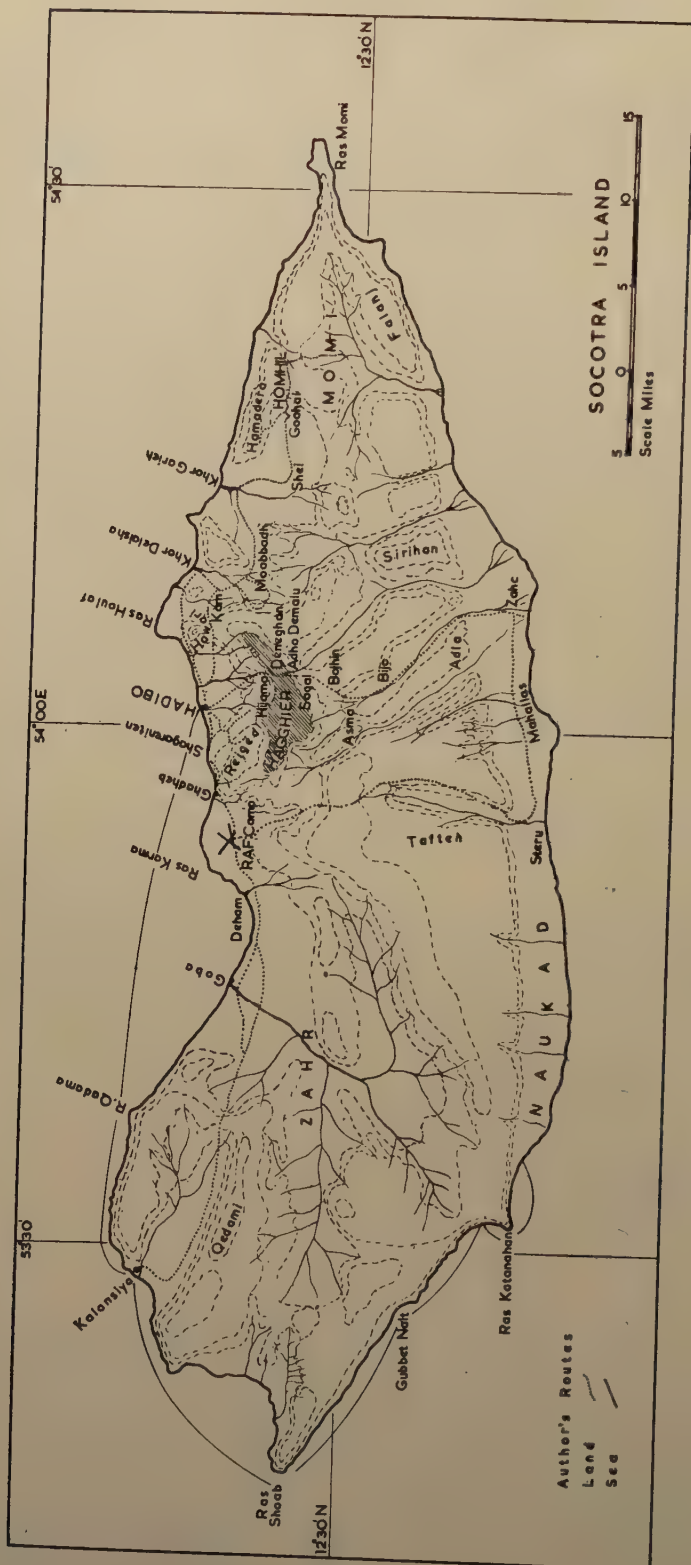
Glomeremus pileatus (Krauss, 1902). (Figs 1–2.)

Eremus pileatus Krauss, 1902: 5.

Eremus pileatus Krauss, 1907: 26, pl. II, figs 9, 9A–D.

Glomeremus pileatus Karny, *Gen. Insect.*, **206** (1937), 115.

Ras Karma, R.A.F. Camp, 26–27 January 1953; 29 February 1953; Hadibo plain, 20–24 January 1953, 5 ♂, 8 ♀.



The series of specimens before us, preserved both dry and in alcohol, shows some difference in the extent of the black pattern from that described and illustrated by Krauss. The only detectable structural difference, however, is that the last tergite in the male is not convex behind, but decidedly truncate. Since Krauss had only one male, it is possible that his description is inaccurate in this respect. Unfortunately, we are informed that the types of Krauss have all been lost and it is no longer possible to check this point. Since all other characters agree, we feel justified in our determination.

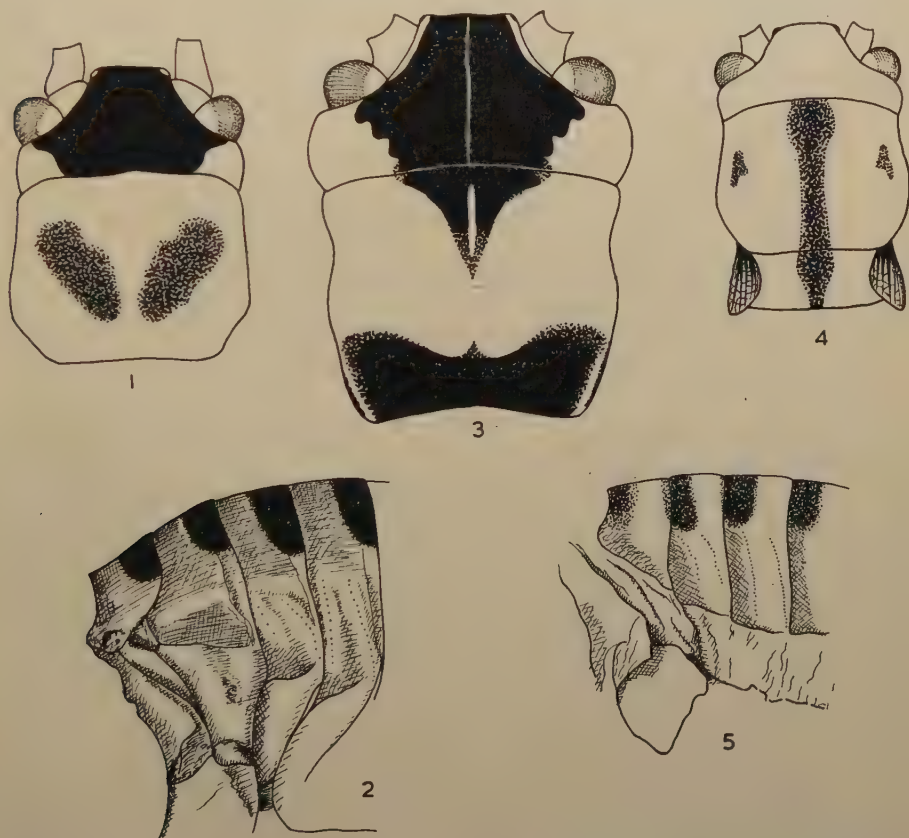
This species is entirely nocturnal and a frequent visitor to light. Several were found by day under rocks and the bark of trees.

G. pileatus emits a persistent stridulation noise, which is just audible, but extremely difficult to locate. The stridulatory mechanism is represented by the two oblique series of minute blackish spinules near the lower ends of the second and the first tergites of the male (Fig. 2).

***Glomeremus capitatus* Uvarov, sp. nov. (Fig. 3.)**

Between R.A.F. Camp and Mahallas, 3000 ft., 26 March 1953, 1 ♂.

Very similar to *G. pileatus*, differing by large head, which is distinctly broader than the pronotum; much less shiny surface; rugulose and distinctly margined fastigium



FIGS. 1-5.—*Glomeremus* spp. 1, *G. pileatus* (Krauss), ♂, head and pronotum; 2, *ditto*, side view of tergites with rows of stridulatory spinules; 3, *G. capitatus* Uvarov, sp. nov., ♂, head and pronotum; 4, *G. mediopictus* Uvarov, sp. nov., ♂, head and pronotum; 5, *ditto*, side view of tergites with rows of stridulatory spinules.

of vertex ; eyes not dark ; pronotum with the black fascia not in the middle, but along the posterior margin ; and by the absence of stridulatory spinules on tergites. Total length 18 mm. ; pronotum 4.0 mm. ; hind femur 4.5 mm.

Glomeremus mediopictus Uvarov sp. nov. (Figs 4-5.)

Deneghan, 3000 ft., 14 March 1953, 3 ♂.

Distinctly smaller than the preceding two species and differing from them by the presence of scale-like elytra, absence of black spot on the head and of black dots on the tibiae, and by different pronotal pattern.

♂.—Surface shiny as in *G. pileatus*. Head not wider than pronotum. Armature of legs as in that species. Small, scale-like elytra present. Last tergite with the posterior margin parabolic and shallowly concave in the middle. Stridulatory mechanism (Fig. 5) similar to that in *G. pileatus*.

Colouration yellowish with castaneous and black markings. Head uniformly yellowish, without black spot and only occiput brownish. Antennae uniformly pale. Pronotum with a black longitudinal median stripe ; black posterior edge and a black-brown spot on the lateral lobe. Mesonotum and metanotum with a black triangular median spot. Elytra with thick castaneous veins. Abdominal tergites with black anterior edges ; these black bands becoming wider at the more posterior tergites, and the last two tergites are wholly ferruginous-black, with the edge of the hindmost being light ferruginous. Legs without black markings.

Total length 14 mm., pronotum 3.5 mm., hind femur 8.0 mm.

Family TETTIGONIIDAE.

Subfamily MECOPODINAE.

Pachysmopoda abbreviata (Taschenberg, 1883).

Mecopoda abbreviata Taschenberg, 1883 : 184.

Mecopoda (Pachysmopoda) abbreviata Karsch, *Berlin. ent. Ztg.*, **30** (1886) : 114, pl. IV, fig. 2.

Pachysmopoda abbreviata Redtenbacher, *Verh. zool.-bot. ges. Wien*, **42** (1892) : 216.

Pachysmopoda abbreviata Krauss, 1907 : 25, pl. II, figs 8, 8A.

Moabbadh plain, 20 m. east of Hadibo, 10-12 February 1953 ; Hadibo plain, 20 January-10 April 1953. Twenty specimens of both sexes.

Taschenberg who described this species from 2 ♂ and 3 ♀ says that the female is green, this colour being lighter on the face and the underside of body, but of a deeper shade on the abdomen dorsally, the hind femora above and the apex of the ovipositor. The male was described as of a lighter, more yellowish, ground colour. However, Krauss already commented that the 11 specimens which he studied had no green colour, and in the present series also no trace of green can be seen, nor has it been observed among the numerous live individuals found in the field. It would appear that the light yellowish-brown basic colouration might very occasionally be replaced by green, as is known to happen in many Orthoptera. The black pattern also varies considerably in its extent.

This is one of the commonest insects on Socotra and it is considered to be a pest by the inhabitants, who even have a special name for it, *Sij'ara*. It is reputed to damage the young flowers and shoots of date palms ; half-chewed inflorescences and fruit were pointed out by the villagers at Moabbadh, who considered that this damage was caused not by the Desert Locust, which was swarming in this locality at the time, but by *Pachysmopoda*.

P. abbreviata occurs on the coastal plains up to an altitude of about 1500 ft. It is entirely nocturnal in its habits, hiding by day in caves, under rocks, in hollows of

trees and similar places. At night several males can usually be heard stridulating in the bushes and can easily be captured by carefully following the noise and using the torch at the last moment. Females were also frequently seen in the vicinity of the males. Although often very numerous, *Pachysmopoda* has always been found singly and does not appear to exhibit any gregariousness. The adults are fully winged but evidently incapable of flight, even when thrown up into the air. One late instar nymph was first found at the end of January and the adults became quite common from mid-March.

Subfamily PHANEROPTERINAE.

Phaneroptera nana Fieber 1853.

Hadibo, 13 February 1953; Deneghan, 14 March 1953; Bojhin, 20 March 1953. Previous records: Hadibo plain, 11 December (Krauss, 1907); Jena Agahan, 2 January (Burr, 1903); Sokotra (Taschenberg, 1883, as *Phaneroptera* sp.).

A frequent visitor to light, but only once seen by day, in the tall grass on the slopes of the Hagghier.

Phaneroptila Uvarov, gen. nov.

Superficially similar to a *Phaneroptera*, with the elytra and wings covering only the abdomen, but differs strongly from that genus by the prominent frontal fastigium, shape of pronotal lobes, non-lobate sternum and boat-shaped male subgenital plate.

Fastigium of the frons laminate, angulate in profile, separated from the fastigium of vertex. Pronotum rounded in prozona, flat in metazona which forms a perceptible, though rounded, angle with the lateral lobe; the latter much longer than deep, with the anterior margin roundly excised, anterior angle about 90° , and the lower margin broadly arched. Elytron of the *Phaneroptera* type, but shortened. Wing a little shorter than elytron, with reduced venation. Anterior coxa armed with a spine; anterior and middle tibia sulcate above, the former with a single external apical spine and open tympani on both sides. Femora unarmed, except posterior one, which bears some small spinules below, and each knee-lobe of which end in a single straight spine. Meso- and metasternum without lobes. Supra-anal plate rounded; cerci moderately long, curved; subgenital plate boat-shaped, without styli.

Phaneroptila insularis Uvarov, sp. nov. (Figs 6, 7.)

Hijama, c. 2500 ft., 15 March 1953, 1 ♂.

Size and coloration as in *Phaneroptera nana*, but pronotum relatively larger and elytra and wings much shorter. Pronotum, legs and abdomen with scattered reddish dots. Supra-anal plate subtransverse, rounded. Cercus weakly curved, somewhat flattened with a short apical spine. Subgenital plate boat-shaped; somewhat longer than its basal width, apex with a small parabolic excision.

Length of body 15 mm.; pronotum 4 mm.; elytron 13 mm.; wings 10 mm.; hind femur 16.5 mm.

Described from a single specimen found among the dense undergrowth in the mixed thickets on the northern slopes of the Hagghier.

Subfamily CONOCEPHALINAE.

Conocephalus bidens Uvarov, sp. nov. (Figs 8, 9.)

Hijama, c. 2500 ft., 15 March 1953, 1 ♂, 2 ♀; Adho Demalu, 3200 ft., 16–17 March 1953, 1 ♀.

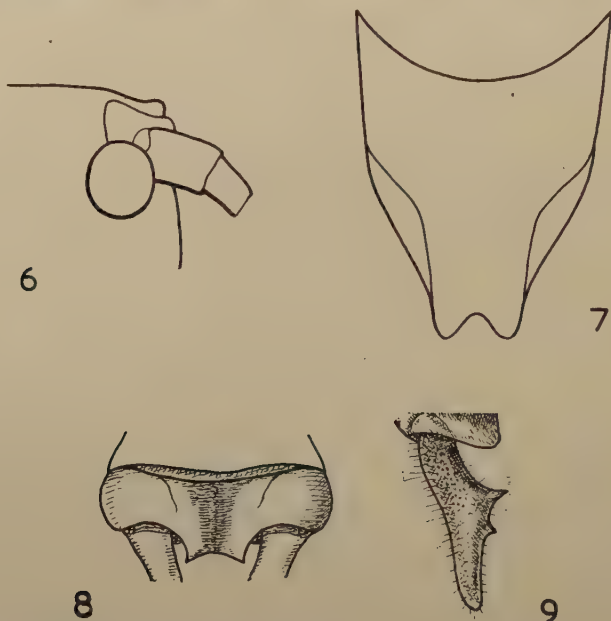
Related to *C. buxtoni* Chopard, 1921 and *C. arabicus* Uvarov, 1933 but differing from them and from other Old World members of this group by the male cercus armed with two spines.

♂ (type).—Size under medium for the genus. Fastigium of vertex, viewed from the front, strongly widened upwards. Lateral pronotal lobe deeper than long, rounded-triangular, lower angle acute; oval callosity hardly developed. Prosternum with a pair of fine spines. Elytron extending well beyond hind knee. Hind femur unarmed. Last tergite with a trapezoidal projection, lateral angles of which bear brown decurved spinules (Fig. 8). Cercus very large, heavy, armed with a large curved tooth placed in the middle and followed by a smaller one (Fig. 9); basal portion cylindrical; apical portion weakly sinuate, tapering. Subgenital plate truncate; styli long.

Colouration as usual in the genus.

♀.—Ovipositor straight, shorter than the hind femur.

Length of body ♂ 14 mm., ♀ 15.5 mm.; pronotum ♂ 4 mm., ♀ 4 mm.; elytron ♂ 18 mm., ♀ 18.5 mm.; hind femur ♂ 14 mm., ♀ 14 mm.; ovipositor ♀ 9 mm.



FIGS 6-7.—*Phaneroptila insularis* Uvarov, gen. et sp. nov., ♂. 6, vertex; 7, end of abdomen.
FIGS 8-9.—*Conocephalus bidens* Uvarov, sp. nov. 8, last abdominal tergite; 9, cercus.

Homorocoryphus nitidulus (Scopoli, 1786).

Hijama, c. 2500 ft. 13 March 1953; Adho Demalu, 3200 ft., 16-17 March 1953; Sagal, 19 March 1953; 3 ♂, 1 ♀.

Found locally common in the tall grasses bordering a small stream in the Haggier mountains, where it occurred together with the less common *Conocephalus bidens*. Nymphs of both these species were much more common than the adults in mid-March.

Family GRYLLIDAE.

Oecanthus chopardi Uvarov, sp. nov.

Oecanthus pellucens Burr, 1903 : 423.

Oecanthus indicus Krauss, 1907 : 27.

Deneghan, 3000 ft., 14 March 1953, 3 ♂ (including the type), 1 ♀; Moabbadh plain, 20 m. east of Hadibo, 10-12 February 1953, 1 ♂.

There is no doubt that both Burr and Krauss misidentified this Socotran species of *Oecanthus*, which differs from *O. pellucens* Scop. by the presence of black dots on the basal segments of antennae, and from *O. indicus* Sauss., which has such dots, by the normal tibial tympanum and cerci, and by the absence of black dots at the bases of tibiae.

♂.—Similar in size to *O. pellucens* Scop., but somewhat more slender. Anterior tibia with the tympanum of normal size. Posterior femur long and slender. Cercus normal, long, projecting well beyond the apex of elytron, but not reaching the tip of the folded wing. Venation as in *O. pellucens*, but the apical area distinctly broader and provided with veinlets.

General colouration pale straw. First and second antennal segments each bear a small brown dot; no postocular dark dot. Elytron with some brown-infumated spots. Posterior femur with the tip of the external knee-lobe black; all tibiae without black markings.

♀.—Ovipositor short, not reaching the apex of the cercus.

Total length ♂♀ 12 mm.; pronotum ♂♀ 2.2 mm.; elytron length ♂ 11 mm., ♀ 12 mm.; elytron width ♂ 4.2 mm.; hind femur ♂♀ 9 mm.; ovipositor ♀ 6 mm.

There is some variation in the brown elytral pattern of the male; the male from Moabbadh plain is marked very heavily, its head, pronotum and antennae beyond the first 2 segments being blackish-brown; the basal segments are, however, lighter in shade and the typical black dots are still perceptible.

Oecanthus chopardi was a frequent visitor to light and, shortly after dark, its continuous, musical trill was one of the common nocturnal sounds in many parts of the island. It could be approached relatively easily, but difficult to find for its small size and cryptic appearance.

This species is named after Professor Lucien Chopard, the eminent specialist in Gryllidae.

? *Landreva* sp.

Landreva spec. nov. ? Burr, 1898: 385.

According to Burr, Bennet's collection included one male, "not sufficiently good for description", which he regarded as possibly a new species of the subgenus *Ectolandreva* Sauss., but the specimen could not be found and the record remains doubtful.

? *Cophogryllus* sp.

Cophogryllus sp., Taschenberg, 1833: 185.

Not found again and the record needs confirmation.

Achaeta rufopicta Uvarov, sp. nov.

Gryllus lepidus Burr, 1903: 422.

Moabbadh plain, 20 m. east of Hadibo, 10–12 February 1953, 1 ♂ (type); Bojhin, 20 March 1953, 1 ♀; Socotra, no locality, 1 ♀.

♂.—Somewhat smaller than *A. domesticus* L.

Face shining blackish-brown, without pale bands; only the ocular spots and antennal pits being light. Clypeofrontal suture broadly arched, its highest part just reaching the level of the antennal pits. Vertex and occiput shining rufous. Cheek behind the eyes whitish. Palpi almost white.

Pronotum mostly brownish, with a pair of large, transverse, pyriform rufous spots; anterior edge of the disc pale yellowish; lateral lobe pale yellowish, except for an elongated brown spot occupying its middle portion.

Elytron blackish basally, infumate in the rest, but with a pale lateral edge, followed on the lateral area by a blackish stripe, while the rest of the area is whitish. Mirror

obliquely transverse, its dividing vein undulated behind the middle ; 5 oblique veins ; apical area rather long, parabolic, with about 5 rows of cells ; lateral area with subparallel veins. Wings long.

All legs light testaceous-yellow. Posterior tibia with 6 inner and 8 outer spines.

♀.—Colouration and pattern as in the male. Ovipositor extending beyond the tip of folded wings and almost reaching the apex of the extended hind tibia.

Length of body ♂ 18 mm., ♀ 17 mm. ; elytron ♂ 12 mm., ♀ 11 mm. ; wing ♂ 22 mm., ♀ 22 mm. ; hind femur ♂ 11 mm., ♀ 12 mm. ; ovipositor ♀ 15 mm.

The specimen without locality label is one of the three females recorded by Burr (1903) as *Gryllus lepidus* Walker, which is an Australian species, only remotely resembling the Socotran one. Krauss (1907) listed a *Gryllus* sp. on the basis of two nymphs, but the species remains uncertain.

A species with a penetrating loud trill. It is terrestrial in its habits and strictly nocturnal, hiding by day in the crevices between and underneath rocks. Very shy and difficult to approach.

Family GRYLLOTALPIDAE.

Gryllotalpa africana (Palisot).

Hadibo plain, 20–24 January 1953 ; Hadibo, 5–8 March 1953.

This mole-cricket is resident in the beds of shallow sandy stagnating permanent streams, overgrown with *Juncus* and sedges, where it digs its burrows close to the edge of the water. Its loud, but mellow, song can be clearly heard at night, but the singer itself remains hidden from view underneath the soil. The specimens mentioned, all males, have been caught by carefully approaching and marking the source of the sound, then suddenly scooping up a handful of sand, which often contained the singer itself.

Family TETRIGIDAE.

Paratettix sp.

A series of specimens, mostly from Hadibo, which it would be impossible to identify specifically, owing to a great confusion in the systematics of the group.

Krauss (1907 : 18) recorded *P. scabra* Thunb. from the Hagghier mountains, but the determination is open to doubt.

The insect was confined to the grassy banks of shallow streams, and was locally very common.

Family EUMASTACIDAE.

Subfamily THERICLEINAE.

Brachytypus insularis (Burr). (Figs 10, 11.)

Plagiotriptus insularis Burr, 1899 : 44.

Plagiotriptus insularis Burr, 1903 : 417–418, pl. XXV, fig. 6.

Brachytypus insularis Kirby, 1910 : Synon. Catal. Orth., III, p. 69.

Ras Shoab, 17 February 1953, 1 ♀ ; Hijama, 15 March 1953 1 ♀ ; Saqal, 19 March 1953, 1 ♀, 1 nymph ; Bojhin, 20 March 1953, 1 ♀ ; Bijo, 21 March 1953, 1 ♀ ; south of R.A.F. camp, 26 March 1953, 1 ♀.

This species is characterized by its arched, short pronotum, partly covering the head from above, rounded obtuse head, short and broad hind femur with the upper crest armed with long spines.

Brachytypus socotranus Popov sp. nov. (Figs 12, 13.)

Moabbadh, 10 February 1953, 2 ♀ (including type), 1 nymph; Hadibo, 8 March 1953 1 ♂, 1 ♀; Adho Demalu, 18 March 1953, 1 ♀.

Differs from *B. insularis* by its pronotum, which is short, not arched and not covering the head. Head acute, raised above the pronotum. Upper part of hind femur armed with shorter spines.

♀ (type).—Antenna short, subequal to length of the eye.

Head acute, projecting above the level of pronotum. Face nearly vertical; frontal ridge slightly convex, meeting the vertex of the head at an acute pointed angle. Fastigium of vertex deeply sulcate. Occiput rounded.

Pronotum compressed laterally; meso- and metanotum exposed; median carina in profile nearly straight; lateral lobes smooth, considerably higher than broad; posterior margin almost straight, anterior margin sinuate, lower ascending forwards; anterior lower angle broadly rounded; the posterior one about 90°.

Valvae of ovipositor very long and slender, finely toothed.

Hind femur moderately broad; lower margin quite straight; upper crest broadly convex, armed with uniform short spines for more than two-thirds of its length; genicular lobes acuminate. Hind tibia longer than the femur, slightly curved. Hind tarsus long and slender; arolium longer than the shorter of the claws, but shorter than the longer one.

Colouration uniformly green or brown, with a wide black dorsal stripe along the abdomen. Hind tarsus purplish. Spines of the hind femur and tibia white, tipped with black.

♂.—Much smaller than the female.

Head projecting as in female. Subgenital plate strongly upcurving, elongate and truncate. Supra-anal plate rectangular, with a short median sulcus. Cercus very short, pointed.

General colouration as in female; dorsal band brownish, continued on the pronotum, while on the abdomen it breaks up into transverse stripes. Hind tibia deep pink.

Total length ♂ 11.5 mm., ♀ 15–23 mm.; pronotum length ♂ 2.5 mm., ♀ 3–5 mm.; pronotum height ♂ 3.5 mm., ♀ 5–6 mm.; hind femur ♂ 9.2 mm., ♀ 9.5–11 mm.

This species appeared to be often associated with *Jatropha unicastata* (Euphorbiaceae), its two colour forms imitating well the light-green and the dry russet-brown of the foliage of this plant. The general distribution of this insect, however, appears to exceed that of the plant, as shown by the specimens from Adho Demalu, 3000 ft. in the Hagghier mountains, whereas *Jatropha unicastata* is a common element of the lower slopes of this granite range up to about 1500 ft., but is rare elsewhere on the island.

Brachytypus dioscoridus Popov, sp. nov. (Figs 14, 15.)

Moabbadh, 10 February 1953, 2 ♀ (including type); Adho Demalu, 18 March 1953, 1 nymph; R.A.F. Camp, 26 February 1953, 1 ♀.

Differs from the preceding species by its elongated pronotum, resembling in this respect *Phaulotypus granti* Burr (Figs 16, 17), from which it can be distinguished by its rounded head, similar to that of *Brachytypus insularis* Burr.

♀ (type).—Antenna shorter than length of eye.

Head rounded, slightly projecting above the level of pronotum. Face vertical; frontal ridge straight, rounded at the fastigium. Fastigium of vertex deeply sulcate. Occiput rounded.

Pronotum elongate, compressed laterally; meso- and metanotum concealed from above; median keel linear, not laminate, in profile broadly rounded; lateral discs finely granulate, considerably broader than high; posterior margin nearly straight,

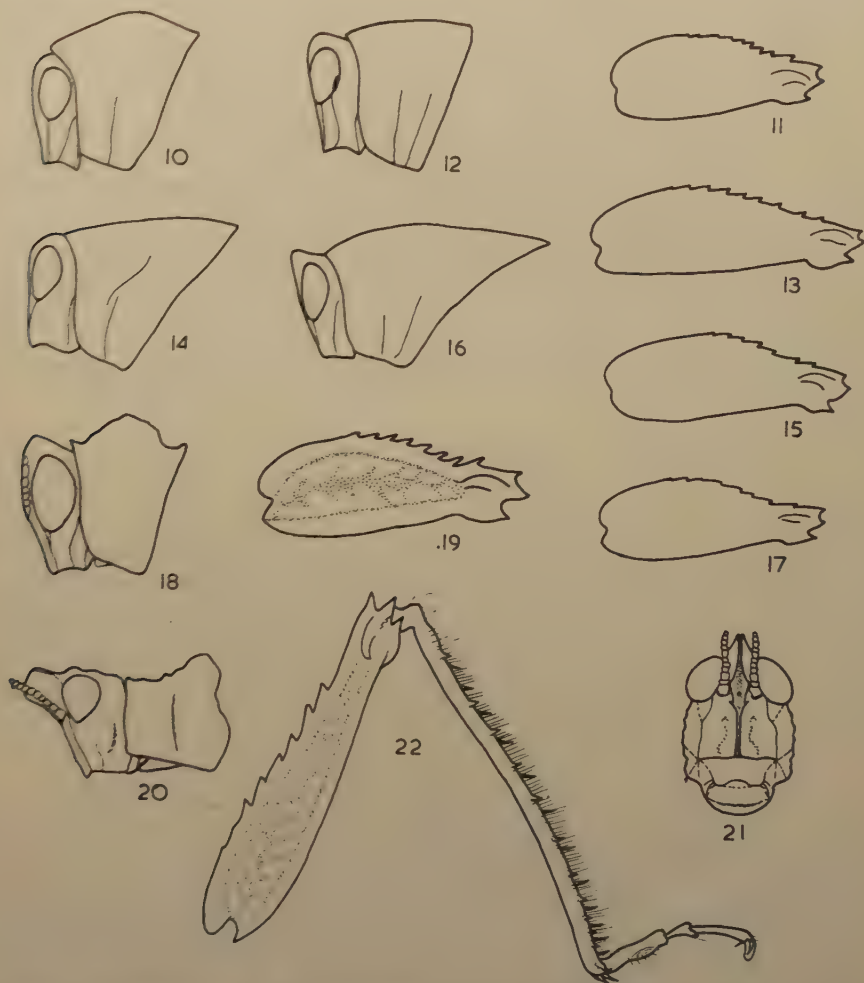
anterior margin sinuate, lower margin ascending; anterior lower angle broadly rounded, posterior one straight.

Valvae of ovipositor moderately long and slender, as in *B. insularis*.

Elytra and wings completely absent.

Hind femur broad; lower margin straight; upper crest suddenly raised in the middle, armed with short appressed spines for slightly more than half its length; genicular lobes acuminate. Hind tibia longer than the femur, outcurved. Hind tarsus long and slender. Arolium shorter than the shorter and longer than the longer claw.

Colouration uniform brownish or greenish. Spines the same colour as the body, tipped with black.



FIGS 10-22.—EUMASTACIDAE. 10, *Brachytypus insularis* (Burr), head and pronotum; 11, *ditto*, hind femur. 12, *B. socotranus* Popov, sp. nov., head and pronotum; 13, *ditto*, hind femur; 14, *B. dioscoridus* Popov, sp. nov., head and pronotum; 15, *ditto*, hind femur; 16, *Phaulotypus granti* Burr, head and pronotum; 17, *ditto*, hind femur; 18, *Clerithes* (?) *nanus* Popov, sp. nov., head and pronotum; 19, *ditto*, hind femur; 20, *Socotrella monstrosa* Popov, gen. et sp. nov., head and pronotum; 21, *ditto*, face; 22, *ditto*, hind femur.

Total length 12.5 mm. ; pronotum length 6.7 mm. ; pronotum height 5.5 mm. ; hind femur 9 mm.

This species appears to have the same distribution as the preceding one, but did not show any obvious association with any particular plant.

***Phaulotypus granti* Burr. (Figs 16, 17.)**

Phaulotypus granti Burr, 1899 : 44.

Phaulotypus granti Burr, 1903 : 418, pl. XXV, fig. 7.

Described from a single female from the Hagg hier mountains, this species has the general habitus of a *Brachytypus*, differing from it by strongly pointed head and elongate pronotum. It is not represented in this collection.

***Clerithes* (?) *nanus* Popov, sp. nov. (Figs 18, 19.)**

Saqal, 19 March 1953, 1 ♂ (type).

A very distinct species differing from all the known ones (C. Bolivar, 1914, *Trab. Mus. Nac. Cien. Nat.*, Madrid, 16 : 48), by its small size, the shape of the pronotum and by the subocular part of the cheek being shorter than the length of the eye. The species is tentatively referred to the genus *Clerithes*, to which it is nearest, but its taxonomic status cannot be established more precisely without a revision of the whole group.

♂ (type).—Very small, testaceous.

Antenna shorter than the eye, filiform. Eye elongate, only moderately prominent, exceeding in height the subocular part of the cheek. Head pointed, projecting above the anterior margin of pronotum, nearly reaching the height of the pronotal crest. Face somewhat oblique. Frontal ridge broadly convex in profile ; surface deeply excavate, margins linear, strongly divergent between antennae and gradually convergent towards apex. Fastigium pointed, acute, deeply excised but without projections ; occiput nearly flat, suddenly broadened behind the vertex.

Pronotum rugulose, moderately and uniformly compressed laterally ; in profile strongly arched in the middle, with both the posterior and anterior margins upturned ; meso- and metanotum exposed. Median keel linear, not laminate ; lateral discs much higher than broad, margins sinuate ; lower margin ascending ; angles rounded, with the anterior one wider than the posterior.

Subgenital plate strongly elongate, narrowed and rounded apically, with a narrow median carinula on the underside and a small shallow excision at the apex. Cerci very short, conical.

Hind femur expanded ; upper crest armed with moderately long spines ; genicular lobes acuminate. Hind tibia uniformly quadrangular, curved, somewhat longer than the femur. Tarsus long and slender ; arolium longer than the shorter claw.

Total length 6.5 mm. ; pronotum length 2.0 mm. ; height 2.0 mm. ; hind femur 5.0 mm.

The single specimen was found on the southern slopes of the Hagg hier mountains, on the open ground between low, fairly sparse vegetation.

Subfamily SOCOTRELLINAE NOV., Popov.

This new subfamily is erected to include the new genus *Socotrella*, described below, which it is impossible to place into any of the known subfamilies of Eumastacidae.

Its appearance almost suggests a Pamphagid (Acrididae), but its short antennae, absence of Krauss' organ, tympanum and elytra, structure of the fastigium, shape of the sternum and the armed femur, indicate that its place is in the Eumastacidae.

The subfamily is characterized by the following features : strongly projecting and deeply cleft fastigium ; upturned hind edge of the pronotum ; heavily sculptured and granulose body, coupled with fairly slender habitus.

Socotrella Popov, gen. nov.

Of medium size, very strongly sculptured all over.

Antenna abbreviated, with shortened segments reduced in numbers. Face strongly oblique in profile, fastigium projecting squarely between the antennae. Frontal ridge with well defined margins ; narrow and sulcate at the clypeus, suddenly widened at the ocellum, then narrowed again with the longitudinal cleft of the fastigium exceedingly narrow and deep ; seen from above, fastigium is triangular, depressed. Occiput rounded, with an incurving raised posterior margin, which causes an arc-shaped gap between head and pronotum.

Anterior margin of pronotum straight, posterior margin strongly upturned, thus while the prozona is horizontal, metazona is strongly ascending, with the mesonotum well exposed ; median carina low, linear ; lateral carinae and transverse sulci obsolescent ; lateral lobe with posterior margin sinuate.

Prosternum with straight carinate anterior margin ; mesosternal lobes widely separated ; metasternal interspace triangular, with very deep pits.

Tympanum, wings and elytra absent. Valvae of ovipositor well exposed, long and slender, both pairs crenulate.

Hind femur with the upper margin slightly wider than the lower, laminate and armed with long spines ; hind knee armed with 3 spines, 1 median and 1 each on the 2 sides of upper lobe ; lower lobe pointed. Hind tibia bent outwardly, somewhat longer than femur ; flattened laterally, with outer face flat and inner laminate ; widened apically, where the tibia is almost square in section ; apical spine present. Hind tarsus moderately long ; the first segment armed with a short spine on the outer surface. Arolium as long as claw. Middle coxa armed with a spine-like projection on the outer surface, while the front coxa bears a similar spine on the inner surface.

Socotrella monstrosa Popov, sp. nov. (Figs 20, 21, 22.)

Adho Demalu, 3000 ft, 17 March 1953, 1 ♀ (type).

♀.—Antenna equal to the greatest diameter of the eye.

Fastigium elongate, triangular, somewhat sloping posteriorly and meeting the vertex at a sharply defined step. Occiput rounded, with a low median carinula and very strongly punctured ; hind margin incurved, moderately raised, notched at the median carinula.

The whole pronotal disc strongly punctured with numerous conical projections. Meso- and metathorax and the first abdominal tergite similarly sculptured and their hind margins somewhat upturned ; other abdominal tergites punctured with the median keel arched and laminate ; sternites all quite smooth.

Hind femur with 7 spines along the upper margin and raised herring-bone pattern on the exterior face. Hind tibia with 12 outer and 13 inner spines including the apical ones and with long dense silky hairs.

Colouration uniformly grey above ; underside brick-red, deepening apically and fading to light buff on the sternum. Underside of hind femur brick-red, upper side with two broad dark fasciae. Hind tibia on the outer and inner sides finely speckled with black.

Total length 27 mm. ; antenna 2.5 mm. ; pronotum 3 mm. ; hind femur 13 mm.

This remarkable species was found only once on the open patch of gravelly ground at an altitude of 3000 ft. at Adho Demalu in the Hagghier mountains. Although the area was searched thoroughly for several hours on two occasions, no more specimens were seen.

In spite of being found on the open ground, the structure and colouration of *Socotrella* suggests that it is phytophilous in its habit, possibly living on the bark of trees.

Family ACRIDIDAE.

Subfamily PYRGOMORPHINAE.

Pyrgomorpha cognata Krauss 1877.

Hadibo, 18–21 January 1953; 1 ♂, 2 ♀; Homhil, 26 February 1953, 3 ♀; Bijo, 21 March 1953, 1 ♀.

This species was recorded by Burr (1903, t.c.: 424) from the island of Abd el Kuri, but it was not previously known from Socotra. It is not uncommon in all drier parts of the island, where it can often be flushed from lower bushes without appearing to be associated with any particular species of plant. It is an occasional visitor to light. Nymphs were seen in February and March.

Physemophorus socotranus (Burr).

Poecilocerus socotranus Burr, 1898: 384.

Poecilocerus socotranus Burr, 1903: 419.

Physemophorus socotranus Krauss, 1907: 21–23, pl. II, fig. 5.

Hadibo plain, 18–21 January 1953, 1 ♂, 7 ♀; Moabbadh, 10 February 1953, 2 ♂; Adho Demalu, 16 March 1953, 2 ♀; Saqal, 19 March 1953, 2 ♀; also numbers of spirit specimens, including nymphs, collected during the above period and roughly in the same localities.

This species was found at all elevations, usually singly. On one occasion, four females were found under the same bush of *Buxus hildebrandtii*, but there appeared to be no connection between the distribution of this plant and that of *Physemophorus*.

The dorsal tubercle described in detail by Krauss (1900, *Zool. Anz.* 23: 155–157, figs. 1–4) in females, is equally well developed in the males, but in the nymphs it only becomes apparent externally in the last instar. The function of this tubercle remained undetermined by field observations. No secretions were produced by the live insect following its capture that could be discerned by sight, smell, or even taste.

Subfamily CATANTOPINAE.

Catantops axillaris (Thunberg).

Catantops versicolor Krauss, 1902: 4.

Catantops versicolor Krauss, 1907: 23.

For full synonymy see Dirsh, V. M. Preliminary revision of the genus *Catantops* Schaum and review of the group Catantopini (Orthoptera, Acrididae). *Publ. cult. Cia. Diamant. Angola*, Lisbon, No. 28, 1956: 11–151, 518 figs.

Hadibo 18–21 January 1953, 4 ♀, 1 ♂; Kalansiya, 18 February 1953, 1 ♀.

Of widespread distribution in Africa and Arabia, this species is abundant on Socotra at lower altitudes, below about 1500 ft. It is certainly one of the commonest insects on the island and occurs in a variety of habitats, but principally where vegetation is denser.

Nymphs were commonly seen during December and January.

***Caloptenopsis glaucopsis orientalis* Schulthess.**

Caloptenopsis orientalis Schulthess, 1898, *Ann. Mus. Mus. Genova*, **39** : 194.

Calliptamus pachypus Krauss, 1902 : 5, syn. nov.

Caloptenus italicus Burr, 1903 : 420.

Calliptamus pachypus Krauss, 1907 : 24, pl. VII, figs 7, 7a.

Caloptenopsis pachypus Uvarov, 1950, *Eos*, Tom. extraord. : 387, 393.

Caloptenopsis glaucopsis orientalis Uvarov, 1950, *l.c.* : 395.

Hadibo, 18–21 January 1953 ; Kalansiya, 18 February 1953 ; Moabbadh, 28 February 1953 ; 8 ♂, 8 ♀.

Krauss described *C. pachypus* from the Haggier mountains and in the British Museum there are 2 ♂, 1 ♀ from Ras Karma, R.A.F. Camp, north coastal plain, 1 November 1945 (J. Stainer), as well as a series of discoloured specimens from Socotra collected by the Balfour expedition in 1880.

[Note by B. P. Uvarov.—A study of the present series showed that my (Uvarov, 1950) previous interpretation of *C. pachypus* was incorrect. It was based on a single female paratype, with somewhat abnormal pronotum, whereas in the present series the median carina is raised not more than in the other subspecies of *Caloptenopsis glaucopsis*. In fact, no differences even of subspecific value, can be seen from *C. glaucopsis orientalis* Schulthess which is widely distributed in the Somali peninsula. In southern Arabia, the species is represented by *C. glaucopsis glaucopsis*, which also occurs in western India.]

In its habits this species is geophilus and its habitat can be described as open, stony or gravelly plains, with only a sparse growth of short annual grasses and herbs. It is commonest on the coastal plains all over the island, but also occurs in similar habitats at higher altitudes, such as the small limestone plateau of Homhil.

Adults were observed from January until April and egg-laying was noticed towards the end of this period. No nymphs were seen.

***Caloptenopsis* (?) *bimaculatus* (Krauss), comb. nov.**

Calliptamus bimaculatus Krauss, 1902 : 5.

Calliptamus bimaculatus Krauss, 1907 : 24.

Moabbadh, 10–12 February 1953 ; Ras Shoab, 17 February 1953 ; Homil, 26 February 1953 ; Hadibo, 8 March 1953 ; Deneghan, 14 March 1953 ; Hijama, 15 March 1953 ; Asma, 15 March 1953 ; 10 m. south of R.A.F. Camp, 26 March 1953 ; Hadibo, early April 1953 ; 11 ♂, 17 ♀.

[Note by B. P. Uvarov.—This species has been omitted from my revision of the genus *Caloptenopsis* (Uvarov, 1950, *Eos*, Tom. extraord. : 385–414), since its generic affinities were not clear from the description based on a single female. The series available now can be clearly referred to this species, but the generic affinities of *C. bimaculatus* still remain somewhat doubtful. The two inner spurs of the posterior tibia are almost equal in length, the lower one being only slightly longer ; and this is a condition intermediate between that observed in *Caloptenopsis* and its allies, on the one hand, and that seen in the group of genera close to *Calliptamus* on the other. The male cercus has only one distinct subapical hook, but there is a second small projection below it, resembling an undeveloped second hook which is characteristic of *Calliptamus*. Very narrow, sulcate vertex is a feature not found in *Calliptamus*, but present in some species of *Caloptenopsis*. Pronotum is distinctly rugulose, and its median carina is deeply notched by two sulci ; although the latter feature is met with in this group of genera, it is not pronounced in either *Calliptamus*, or *Caloptenopsis*. A new genus may be required to accommodate *C. bimaculatus*, but the whole group Caliptamini is not yet sufficiently studied to justify this and the

species is tentatively transferred to *Caloptenopsis*, with which it agrees in the character of the male cercus better than with *Calliptamus*.]

In contrast to the preceding species, *C. bimaculatus* frequents the more wooded parts of Socotra, where it has been found at all elevations. The two species of the genus, thus, seldom occur side by side.

It is not at all uncommon and its brilliant rose hind wings and the crackling noise which it emits in flight, render *C. bimaculatus* one of the most conspicuous insects on the island.

Nymphs were common in January and February and the final moult appeared complete by early March.

Dioscoridus Popov, gen. nov.

Under medium size, body cylindrical, somewhat depressed; glabrous with shallow puncturation; apterous.

Antenna filiform, moderately long. Head short and broad, not prominent above pronotum. Face strongly oblique; frontal ridge narrow with well defined margins, protruding forward at the fastigium; fastigium of vertex strongly sloping forward, narrower than long. Eyes very prominent, less than one and a half times as deep as long; interocular space not exceeding the width of the antenna.

Pronotum completely rounded, of uniform width throughout; anterior margin somewhat projecting forward, sinuate; posterior margin straight, not quite covering the mesonotum; lateral carina only represented by two slight rounded projections. Only the posterior transverse sulcus distinct, with the metazona less than one quarter of the length of prozona; other sulci ill-defined, incomplete. Lateral lobe an almost regular semicircle. Prosternal tubercle short, conical; mesosternal lobes as broad as long, rounded; metasternal lobes joined in male, slightly separated in female. Tympanum moderately large, open, shallow.

Male subgenital plate acute, somewhat upturned; cercus small, simple, conical.

All femora somewhat swollen. Hind tibia rounded, of more or less uniform width, with an inner and an outer apical spine. Arolium rounded, longer than half the length of claws.

Dioscoridus depressus Popov, sp. nov. (Fig. 23.)

Ten miles south of R.A.F. Camp, 26 March 1953 1 ♂ (type); Adho Demalu, 16 March 1953, 1 ♀; Hadibo plain, early April 1953, 1 ♂; Shoab, Moabbadh, Bojhin, February, March, 7 nymphs.

♂ (type).—Antenna more than half as long again as head and pronotum together. Frontal ridge sulcate with wavy margins, suddenly constricted below ocellum, then widened and obsolescent towards clypeus. Fastigium of vertex rhomboid, narrowly sulcate. Occiput broadly rounded, without a median carinula.

Surface of pronotum uniformly and shallowly punctured; crossed by 3 broad transverse sulci, only the posterior one being complete; two ill-defined swellings in front of the first sulcus represent the lateral carinae.

General colouration dark-brown with darker broad lateral bands and a white dorsal stripe, beginning at the fastigium. Hind femora uniform dark brown; hind tibia brownish, with short silky hairs.

♀.—Larger and a little more robust than the male, eyes less prominent. Antenna slightly less than half again the length of the head and pronotum together. Colouration dirty brownish-grey, sometimes with indistinct dark markings.

Total length ♂ 22 mm., ♀ 24 mm.; pronotum ♂ 5 mm., ♀ 5.5 mm.; hind femur ♂ 14 mm., ♀ 15 mm.

It is difficult to decide on the true affinities of this insect, as it has no near relative. It has some superficial resemblance to some of the arbusticolous genera of Catanto-

pinae, well represented in East Africa, with a few close relations in SW. Asia. In its closely-spaced eyes, rounded pronotum and apterism it resembles the South American genus *Sitalces*, although due to some structural differences, such as the absence of the inner apical spine on the hind tibia in the latter genus, the resemblance may be a purely superficial one.

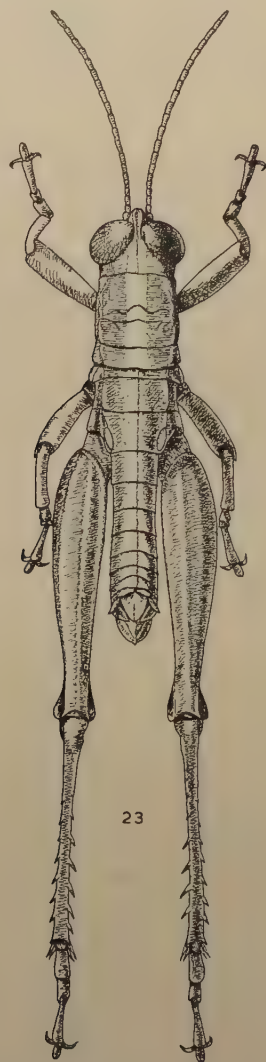


FIG. 23.—*Dioscoridus depressus* Popov, gen. et sp. nov., ♂.

Although found in several widely separated localities *Dioscoridus depressus* did not appear to be a common species. A colony of nymphs was first found under the bark and in the cracks of a dead *Boswellia* tree and subsequently other nymphs and adults were found under stones, bark of trees, as well as on the open ground. In its habits, therefore, *Dioscoridus* resembles the genus *Allaga*, members of which are found in southern Arabia and in Somaliland almost exclusively under bark of trees. Although never recorded at light, this species may well be nocturnal in its habits.

Cataloipus brunneri Kirby 1910.

Cataloipus oberthüri Burr, 1903 : 420, pl. XXV, figs. 2, 2a (*partim*).

Cataloipus brunneri Kirby, 1910, *Syn. Cat. Orth.*, 3 : 557.

Kalansiya, 18 February 1953 ; Adho Demalu, 16 March 1953 ; 8 ♂, 6 ♀. Recorded by Burr from Homhil and Hadibo plain.

One of the female specimens determined by Burr as *C. oberthüri* and preserved in the British Museum, is *Thisoicetrus caerulescens* (Stål), but one male and one female nymph belong to the genus *Cataloipus*. Kirby gave a new specific name, *brunneri*, to the Socotran species ; although he did not describe it, the reference to Burr's figures makes the name valid and Kirby must be regarded as the author, since his reference to Bolivar (MS.) means merely that the name was suggested by I. Bolivar, probably in a letter. Systematics of this genus being in a chaotic state, it would be useless to attempt a critical determination of the Socotran species, and it may be called *C. brunneri* Kirby until the genus is revised. This course is preferable to that proposed by Uvarov (1921, *Trans. ent. Soc. Lond.*, 140), who synonymized *C. brunneri* with *C. somalicus* (Rehn), without sufficient material.

Cataloipus brunneri was confined to *Juncus* and sedge marshes along and in the mouths of some of the streams. Although it was very abundant locally, as at Kalansiya and Adho Demalu, this species has never been encountered outside the narrow confines of its habitat.

Late-instar nymphs and adults in various stages of maturation were encountered in above localities during February and March.

Thisoicetrus caerulescens (Stål).

Cataloipus oberthuri Burr, 1903 : 420 (*partim*).

Bibulus brunni Uvarov, 1921, *Trans. ent. Soc. Lond.*, 131.

Thisoicetrus caerulescens Popov, 1950, *Proc. R. ent. Soc. Lond.* (B), 19 : 134.

One female of this species was found among the specimens from Socotra, determined by Burr as *Cataloipus oberthüri* (now *C. brunneri*—see above). Correct synonymy of this insect was established by Popov (1950). This record remains unique, as *Thisoicetrus caerulescens* is not represented in the 1953 collection from Socotra.

Thisoicetrus sp.

Another species of *Thisoicetrus*, similar to *T. rantae* Uv. of southern Arabia and Somaliland, was seen but not captured at Ghublet Nait.

Schistocerca gregaria (Forskål).

The presence of swarms of the Desert Locust on the island of Socotra, was the main reason for the present visit and forms the subject of a separate paper (Popov, in press). It is interesting to note that previous expeditions did not record the occurrence of this species on the island.

Anacridium melanorhodon arabafrum Dirsh.

Acridium tataricum var. *moestum* Burr, 1903 : 421.

Anacridium melanorhodon arabafrum Dirsh, 1953, *Eos*, 24 : 7-69.

Moabbadh, 10-12 February 1953, 1 ♂ ; Homhil, 26 February 1953, 1 ♀ ; Hadibo, early April 1953, 1 ♂.

Occasional in the more wooded parts of the island.

Cyrtacanthacris tatarica (L.).

Acridium tataricum Burr, 1903 : 421.

Hadibo, 21 January 1953, 1 ♂ ; Moabbadh, 10 February 1953, 1 ♀.

A species widely distributed in Africa and Asia, occurring on both sides of the Red Sea and the Gulf of Aden.

Subfamily OEDIPODINAE.

Sphingonotus canariensis Saussure.

Four ♂ and 3 ♀ were collected on the open gravel plain at the Royal Air Force Camp (Ras Karma), on 26 January 1953 and 2 ♂ and 2 ♀ in a similar habitat on Hadibo plain in early April 1953.

This species has a very wide distribution from Cape Verde and Canary Islands to Somalilands, Arabia and East Africa. Its occurrence on Socotra, therefore, was only to be expected.

The characters on which Mistshenko (1936, *Eos*, XII, p. 100) based his subsp. *orientalis*, described from Sana'a, Yemen, appear to be individual.

Sphingonotus albipennis Krauss.

[*Note by B. P. Uvarov.*—This species was originally diagnosed by Krauss from Professor Simony's collection as taken on Socotra, but in the later redescription (1907) he correctly recorded the type locality as the Abd el Kuri island. Mistshenko (1936, *Eos*, XII, p. 157), has examined Krauss' type and also recorded the locality correctly, but he had before him also a specimen from the British Museum, determined by Burr as *Sphingonotus coerulans* and labelled "Sokotra". This was one of the specimens belonging to the Forbes collection, made partly on Socotra, partly on Abd el Kuri, but the whole of which was labelled in the British Museum as from Socotra. Two more specimens belonging to the same collection, bear identification labels *Sph. coerulans*, and the locality labels Abd el Kuri, 27 February 1898 and 5 December 1898. All are undoubtedly the specimens erroneously recorded as *S. coerulans* from Abd el Kuri by Burr (1903). Therefore, *S. albipennis* remains known only from that island, and must be excluded from the Socotran list.

S. albipennis is extremely close to *S. savignyi* Sauss., differing from it only in the absence of a dark wing-band, which is often weak in *S. savignyi*, and it may represent merely an island subspecies of *S. savignyi*. The latter species was also recorded by Burr (*t.c.*) from Abd el Kuri, but no specimens with such a label have been found either in the British or the Liverpool Museums, and Burr must have mistaken a darker specimen of *S. albipennis* for *S. savignyi*.

However, the apparent absence of *S. savignyi* from both Socotra and Abd el Kuri is curious, since this is one of the most actively flying and widely distributed species of the genus.]

Sphingonotus turkanae Uvarov.

Ras Karma, R.A.F. Camp, 26 January 1953, 5 ♂, 1 ♀ ; Bijo, 21 March 1953, 1 ♀.

No difference could be found between the type and the series from Socotra. The present record extends the known distribution of this species which was known from the Rift Valley in Kenya through Somalilands to southern Arabia, as represented by specimens in the British Museum collections.

S. turkanae was found on the open gravelly plains at all elevations together with *S. canariensis*.

***Sphingonotus gangblaueri* Krauss.**

Sphingonotus gangblaueri Krauss, 1907: 21, pl. II, fig. 4.

Hadibo, 18–21 January 1953; R.A.F. Camp, 26–27 January 1953; Moabbadh, 10–12 February 1953; Kalansiya, 18 February 1953; Bijo, 21 March 1953; Naukad, 23 March 1953; Hadibo, early April 1953; 22 ♂, 12 ♀.

Described by Krauss (1907) from a single male, on which Mistshenko's (1936, *Eos*, XII, p. 155) redescription is also based. While in the majority of specimens now available hind wings are bluish-hyaline, in some there are faint indications of an interrupted smoky fascia. The darkening of the veins in the apical part of the wing, mentioned by Mistshenko, is continued in some of the specimens along the outer edge of the wing.

Measurements of females, not previously described, are as follows: total length 24–27 mm.; pronotum 5–6 mm.; elytron 25–27.5 mm.; hind femur 11–13 mm.; hind tibia 10–11.5 mm.

This species was common in coastal gravel plains and encountered to 700 m. altitude. Like the preceding species it keeps to bare gravelly and sandy patches of soil, where it is very difficult to see due to its protective colouration. Nevertheless it is easily spotted by listening for the loud crackling, which it emits in flight, like species of *Helioscirtus*.

***Wernerella insularis* Popov, sp. nov. (Figs 24–26.)**

Limestone plateau south of R.A.F. Camp, 26 March 1953, 3 ♂, 4 ♀ (including type); Ras Shoab, 17 February 1953; Homhil, 26 February 1953; Bijo, 21 March 1953; Naukad, 23 March 1953; Hadibo plain, early April 1953, 15 ♂, 3 ♀.

The genus *Wernerella* is an off-shoot of *Sphingonotus*, differing from it in some specializations of the head and pronotum. So far it was believed to be confined to the Canary Islands and the Atlantic coastal zone of southern Morocco, with one species in South Africa, and the new species establishes yet another link between the fauna of the Canaries and that of Socotra.

Wernerella insularis differs from the other species of the genus by its very broad, fasciated hind wings, the shape and striking deep blue colour of the supra-anal plate in males and the shape of the hind femur. It appears to be nearest to the Canarian *Wernerella aspera* (Brullé, 1838) differing from it mainly by wider wings and continuous intercalary vein.

♀ (type).—Antenna nearly as long as head and pronotum together. Face practically vertical, strongly punctured and rugulose; lateral facial keels well defined, wavy, strongly divergent downwards and nearly reaching the clypeus. Frontal ridge suddenly expanded between the antennae and the ocellum, concave especially at the ocellum, but becoming flat and obsolescent half-way down to clypeus. Fastigium of vertex sloping forward, shallowly concave and rugulose; foveolae elongate, roughly kidney-shaped, with acute wavy margins.

Pronotum distinctly sellate, strongly rugose and punctured. Anterior margin dentate. First transverse furrow deep, sinuate, the second obliterate in the middle, the third deep and irregular. Prozona half the length of metazona, the latter distinctly convex, rectangular behind, with wavy margins; shoulders distinctly raised. Median carina thick and gibbose in front of the first furrow, scarcely perceptible behind it. Lateral carina distinctly raised, but irregular in front of the first furrow, indistinct behind it. Lateral pronotal lobes much deeper than broad; lower margin strongly sinuate and ascending; hind angle broadly rounded; hind margin strongly wavy.

Elytron five times as long as broad, anterior margin broadly and regularly convex; venation moderately dense; intercalary vein well developed, subsinuate and very close to the discoidal vein in its apical half.

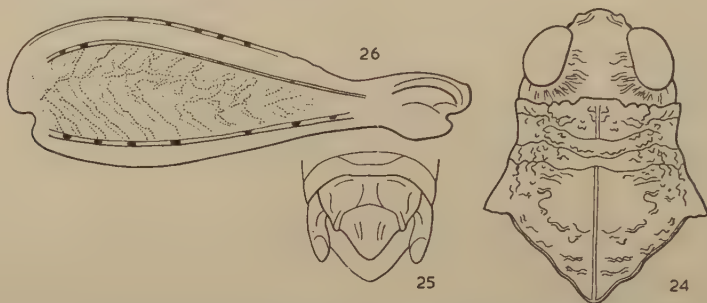
Hind wings, length/width, 1.5.

Hind femur heavy, upper margin very slightly wavy, laminate and raised throughout, but suddenly lowered near the knee.

♂.—Male supra-anal plate deep indigo-blue, triangular, pointed, with two small projections half-way along the outer margins.

Colouration ochraceous-brown or greyish; face whitish. Elytra with the basal third darker and with indistinct large, darkish spots elsewhere. Hind wings sky-blue with a dark fascia, not quite reaching the hind margin and sometimes broken up into 3 distinct spots. Hind femur on the inner side jet-black in the basal half; with a preapical black spot; yellow elsewhere. Hind tibia bluish.

Wernerella insularis was not uncommon in all barren habitats from the limestone plateau to the sea level, where it occurred on bare patches of gravel together with *Sphingonotus gangblaueri* and *S. canariensis*.



FIGS 24-26.—*Wernerella insularis*, Popov, sp. nov. 24, head and pronotum. ♀; 25, supra-anal plate, ♂; 26, hind femur, ♂.

Acrotylus incarnatus Krauss.

Acrotylus longipes Burr, 1903 : 419.

Acrotylus longipes var. *incarnata* Krauss, 1907 : 19.

Acrotylus longipes var. *meruensis* Sjöstedt, *Ark. Zool.* 24A (1) : 66, pl. 5, figs 3a, 3b (syn. nov.)

Hadibo, 18-21 January 1953, 5 March 1953; Moabbadh, 10 February 1953; Kalansiya, 18 February 1953; Bijo, 20 March 1953; 10 m. south of R.A.F. Camp, 26 March 1953, 5 ♂, 5 ♀.

[Note by B. P. Uvarov.—This rose-winged *Acrotylus* was mentioned by Burr as a colour form of *A. longipes*, and later described by Krauss as var. *incarnata*. All the Socotran specimens have rose-coloured wings, but they do not differ morphologically from the East African *A. longipes* var. *meruensis* Sjöstedt, in which wings are either rose or yellow. On the other hand, the Mediterranean *A. longipes*, which is larger and more heavily built, appears specifically distinct from *incarnatus* and the latter should be regarded as a species, at least until the genus is revised.]

This insect was most common in the sandy areas of the coastal plains, frequent in the date gardens and has also been found in the Haghghier mountains.

Oedaleus senegalensis Krauss.

Moabbadh, 10 February 1953; Hadibo plain, 18-21 January 1953; Hadibo plain, early April 1953, 2 ♂, 3 ♀.

Not uncommon on the coastal plain in the short grass—low scrub vegetation belt. This species is widespread in Africa and SW. Asia, inhabiting the short grass savanna.

Scintharista forbesii (Burr).

Dissosteira forbesii Burr, 1899 : 44.

Dissosteira forbesii Burr, 1903 : 418, pl. XXV, fig. 1.

Quiroquesia forbesi Krauss, 1907 : 19, pl. II, figs 2, 2A.

Hadibo, 24 January 1953 ; Moabbadh, 10 February 1953 ; Homhil, 26 February 1953 ; Asma, 21 March 1953 ; Bojhin, 20 March 1953 ; 8 ♂, 6 ♀.

This strikingly handsome Acridid has been encountered on dry, gravelly hillslopes at all altitudes. It is entirely geophilus in its habits and easily attracts attention by its inky-black hind wings and the loud, sharp cracking noise it often produces in flight.

Nymphs were seen in January and February.

Aiolopus thalassinus (Fabr.).

Hadibo, 18–21 January 1953 ; Hadibo, 13 February 1953 ; Adho Demalu, 16 March 1953 ; Hadibo, early April 1953 ; 1 ♂, 5 ♀.

Predominantly phytophilus, this species was found to be common along the grassy banks of streams at all altitudes. It was also occasionally recorded at light.

Subfamily TRUXALINAE.

Ochrilidia kraussi (I. Bolivar).

Ras Shoab, 17 February 1953 ; 2 ♂, 2 ♀.

The Socotran specimens differ from the typical *O. kraussi*, from the Sàhara, in being smaller and shorter, and particularly in the metazona of pronotum being as broad as long, whilst in the typical specimens it is considerably longer, but we hesitate to separate the Socotran specimens on the basis of this difference alone. Some of the specimens in the British Museum collection from Somaliland resemble closely those from Socotra and it is possible that in time this species may be divided into a number of recognizable subspecies or races.

This species was common in tufts of the spiky grass *Heleochloa dura*, fringing the low coastal dunes at Ras Shoab, at the south-west corner of the island, but it was not seen elsewhere. Mature and immature adults and nymphs were observed in mid-February.

Ermia Popov, gen. nov.

Ermia is a small insect with the general habitus of a *Raphotittha*, but the resemblance is purely superficial and it is readily distinguished from that genus by its ensiform antennae and the long and narrow foveolae of vertex, completely concealed from above. In these respects it closely approaches *Ochrilidia*, from which it differs by the habitus, the rudimentary wings and elytra and the structure of pronotum.

The generic name is derived from the Socotri name "*Ermio*", for a grasshopper.

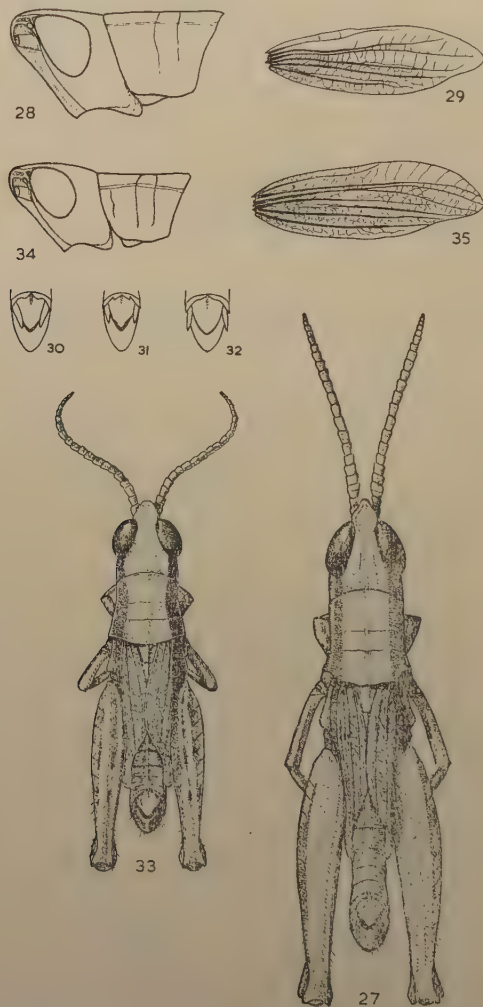
Antenna ensiform, moderately long. Head not, or slightly raised above pronotum. Face strongly oblique ; frontal ridge straight in profile, sulcate and marginate. Apex of head in profile rounded. Fastigium of vertex strongly projecting forward, somewhat longer than broad, with well defined margins. Foreolae of vertex well marked, completely lateral and not visible from above, elongate. Eyes elongate, oblique ; interocular distance twice the width of the frontal ridge between antennae.

Pronotum subcylindrical, very slightly compressed laterally ; disc obtusely tectiform. Median carina linear, cut only by the posterior sulcus well behind its middle. Lateral carinae low, straight or inflexed and diverging, sometimes partly obliterated, interrupted by two sulci. Hind margin broadly rounded, sometimes weakly excised. Lateral lobes trapezoidal, slightly longer than high ; lower margin sinuate ; hind angle rounded, rather more than 90°. Mesosternal lobes and their interspace transverse ; metasternal lobes contiguous in both sexes.

Elytra reduced and in females do not meet dorsally. Hind femur moderately heavy, projecting slightly beyond the tip of the abdomen ; inner side with stridulatory pegs. Hind tibia somewhat shorter than the femur ; inner spines longer than the outer, regularly curved. Arolium small, rounded, triangular, about half the length of a claw. Male cercus simple, pointed ; supra-anal plate acute. In female, supra-anal plate not covering the ovipositor.

Ermia variabilis Popov, sp. nov. (Figs 27–32.)

Homhil, 26 February 1953, 7 ♂ (including type), 9 ♀ ; Hijama, 15 March 1953, 2 ♂, 6 ♀ ; Adho Demalu, 18 March 1953, 6 ♂, 4 ♀ ; Bijo, 21 March 1953 ; 1 ♀ ; south of R.A.F. Camp, 26 March 1953, 3 ♀.



FIGS 27–32.—*Ermia variabilis*, Popov, gen. et sp. nov., 27, ♂ ; 28, head and pronotum, ♂ ; 29, elytron ♂ ; 30–32, variation of last abdominal tergite ♂.

FIGS 33–35.—*Ermia somalica*, Popov, sp. nov. 33, ♂ ; 34, head and pronotum ♂ ; 35, elytron, ♂.

The series of 15 ♂ and 23 ♀ from a number of localities which have served for the description of the new genus *Ermia*, exhibit a considerable degree of variation, not only in colouration, but also in some of the structural characters. Although the extreme forms appear to be quite different, they are connected by intermediate forms in series from the same or other localities. Therefore, it is preferred to regard the variation of the present series as intraspecific.

The following description is based on the type: deviations seen in the paratypes, will be indicated in brackets.

♂ (type).—Antenna ensiform, expanded in the basal third, as long as the head and pronotum (in two of the males from Adho Demalu, antenna is nearly half as long again, but in two other males from the same locality, it is as short as in the type, while in two more they are intermediate: the longer the antenna, the less dilated it appears to be). Face strongly oblique. Frontal ridge in profile straight (or very slightly concave), distinctly sulcate and coarsely punctured; margins raised, slightly divergent below the ocellus, and parallel between the ocellus and the base of the antenna. Apex of head in profile with acute, but rounded, angle. Fastigium of vertex horizontal, elongate, surface concave, with a fine median carinula; lateral margins well marked, meeting at an acute rounded angle in front, gradually converging and obsolescent behind. Foveolae of vertex well impressed, narrowed in front, more than twice as long as their maximum width, with all angles rounded. Eye oblique, subtriangular.

Pronotum very feebly compressed laterally; median carina low, linear, cut by the hind sulcus only; prozona nearly twice as long as the metazona; lateral carinae well marked, cut by two sulci, parallel in front and slightly diverging behind the first sulcus (in some of the paratypes, the lateral carinae are less well marked, sometimes almost completely obliterated, and also more inflexed); surface shallowly punctured throughout; hind margin very broadly rounded, shallowly notched in the middle (this notch is absent in some of the paratypes). Lateral lobes coarsely and shallowly punctured.

Elytra extending a little beyond the middle of the abdomen, their shape and venation shown in Fig. 29. Wings lateral, not reaching hind margin of tympanum. Last abdominal tergite (Fig. 30) with two rounded projections (in one of the paratypes these projections are acute, Fig. 31, while in some others they are broadly rounded, Fig. 32).

General colouration dark stramineous, with dark lateral postocular stripes continuing along the sides of the pronotum and the elytra (these stripes vary considerably in width and in some of the paratypes they are absent, this usually being associated with darker ground colour and indistinct spotted pattern). Hind femur ivory-brown outside (in some of the paratypes it is on the contrary darker outside, with an indistinct dark fascia on the upper side, while in others it is uniformly dark-brown). Hind tibia uniformly dark-grey, shiny.

♀.—More robust than male. Antenna somewhat shorter than head and pronotum. Elytra not quite reaching the second tergite. Colouration even more variable than in males, presenting in addition to the patterns mentioned above, a white and dark speckling associated with an X-shaped pattern on the pronotum, when the lateral pronotal carinae become obliterated. In another form, instead of the postocular stripe, the lateral pronotal carinae are margined by black on the dorsal side; yet in others there is a median white dorsal line along the whole body.

Total length, ♂ 12–14 mm., ♀ 15–21 mm.; pronotum, ♂ 3 mm., ♀ 4 mm.; elytron ♂ 5 mm., ♀ 5 mm.; hind femur ♂ 8.5 mm., ♀ 12 mm.

Ermia variabilis has only been found above an altitude of about 2000 ft., where it was recorded in many parts of the highlands, both on the limestone plateau and the granite block of the Hagghier. Its habits are similar to those of *Leva socotrana* (see below) and the two were not infrequently found together. The main apparent difference was that, while *Ermia* was equally common on the taller *Hyparrhenia* and

Themeda grasses and the bare patches of ground, *Leva* avoided the denser vegetation. Nevertheless, *Ermia* is much less phytophilus than its near relative, *Ochridia*, and when pursued, it was never seen to hide inside a clump or behind a blade of grass, but escaped by hopping and alighting on the ground.

Nymphs were seen in numbers at Homhil in February, but not in March or April.

Another species of this new genus, of which *E. variabilis* is the type-species, occurs in the Somaliland and the opportunity is taken to describe it below.

***Ermia somalica* Popov, sp. nov. (Figs 33–35.)**

Among a collection of Orthoptera made by G. Popov, D. J. Greathead and other members of the Desert Locust Survey Reconnaissance Unit, during winter 1953–54 in the Somaliland Protectorate, there are two adult males and two female nymphs taken on 20 December 1953 in the highlands near Erigavo, which undoubtedly belong to the genus *Ermia*.

The species from Somaliland is quite distinct, differing from the Socotran *E. variabilis* by the following characters :

♂ (type).—1. Head nearly as long as pronotum, while in *E. variabilis* it is distinctly shorter. Apex of head more rounded ; foveolae of vertex moderately impressed of equal width throughout, half as long as wide. Eye oval, not subtriangular as in *variabilis*.

2. Last abdominal tergite with rounded margins, not wavy or toothed as in *variabilis*.

3. Elytra reaching the edge of the penultimate tergite i.e. nearly half as long again as in *variabilis*, venation see Fig. 36.

4. Smaller than *variabilis* : total length 10 mm. ; pronotum 2.5 mm. ; elytron 5 mm. ; hind femur 6 mm.

The two males of *Ermia somalica* also show other differences from *E. variabilis*, particularly in the shape of pronotum ; for instance in neither of them is the hind margin notched and the lateral carinae are inflexed in both.

Ermia somalica was collected in a habitat rather similar to that of *Ermia variabilis* on Socotra (see Pl. 8). The area was an elevated part of the limestone plateau in the vicinity of Erigavo, here reaching a height of about 6000 ft. The vegetation was represented by xerophytic elements with a predominance of succulents ; the dominants were *Dracaena*, *Aloe* sp., *Senecio* (*Kleinia*) *longiflorus*, with a sprinkling of annual herbs. The specimens were found among the moderately tall grass bordering the edge of a small dry runnel.

Ermia somalica was recorded only from this locality and its scarcity may have been seasonal. It does not appear to be a common species, since it is not represented in other collections from the Somaliland Protectorate.]

***Leva socotrana* Popov, sp. nov. (Fig. 36.)**

Hadibo plain, early April 1953, 1 ♂ (type), 1 ♀ ; Hadibo, 5–8 March 1953 ; 18–24 January 1953 ; Homhil, 26 February 1953 ; Moabbadh, 10–12 February 1953 ; Deneghan, 14 March 1953 ; Naukad, 23 March 1953 ; Hijama, 15 March 1953 ; 10 ♂, 18 ♀.

Differs from the known species of the genus by its slender habitus, by the elytra and wings extending well beyond the hind knees and by the well developed lateral pronotal carinae. In these respects, it resembles more a *Stenohippus*, but on the basis of the accepted generic characters the new species must, at least temporarily, be referred to *Leva*.

The species shows a considerable degree of structural and colour variation in the elytra, which in males may project from about one-eighth to one-third of their length beyond the hind knees ; in the extent of exposure of temporal foveolae



FIG. 1.—Habitat of *Ermia variabilis* on the middle slopes of the Haggier range, Socotra.



FIG. 2.—Habitat of *Ermia somalica* in the highlands near Erigavo, Somaliland Protectorate.

when seen directly from above : and in the lateral pronotal carinae being interrupted either by 2 or 3 transverse sulci.

♂ (type).—Antenna filiform, somewhat compressed laterally, slightly longer than head and pronotum together. Head nearly as long as pronotum, well raised above its level. Face oblique ; frontal ridge in profile straight, forming an obtuse rounded angle with the vertex ; surface shallowly sulcate and sparsely punctured ; margins well raised, parallel between the antennae, converging towards the apex and diverging below the ocellus. Fastigium of vertex pentagonal, deeply excavated, with well defined margins and slightly longer than broad. Foveolae of vertex partly visible from above, trapezoidal with well raised margins and moderately rounded angles.

Pronotum sellate ; metazona slightly longer than prozona, obtusely angulate behind. Median carina well marked, interrupted by the hind sulcus only. Lateral carinae distinct throughout, incurved, interrupted by all three sulci.

Elytron narrow, exceeding the hind knee by the length of the pronotum.

General colouration dark greyish-brown above, light buff below. Face and cheeks light brown : occiput darker brown with two dark postocular fasciae, extending along and below the lateral pronotal carinae. Pronotum above uniformly dark brown ; lateral lobes below the dark fascia, light brown. Hind femur buff, with two interrupted dark fasciae on the upper side ; outside with an indistinct whitish pattern. Hind tibia light dirty brown.

Female similar to the male, but larger.

The type is the darkest colour form. The paratypes show several other colour forms as known in other genera of the group Chorthippi, e.g. : stramineous, with broad dark lateral stripes ; or mottled grey-brown, with numerous dark grey blotches and spots on a light buff background. The last form sometimes has a pronounced X-pattern on the pronotum.

Length of body, ♂ 11.5–13 mm., ♀ 14–17 mm. ; pronotum ♂ 2.5 mm., ♀ 3 mm. ; elytron, ♂ 11–13 mm., ♀ 13–16 mm. ; hind femur ♂ 8 mm., ♀ 10 mm.

Leva socotrana was very common in practically all parts of the island. It inhabits the open dry hill slopes and plains. The male frequently sits on a prominent stone, or an open patch of ground, stridulating a high interrupted note. The insect can thus be spotted with relative ease, whilst otherwise, due to its small size and protective coloration, it can easily escape notice.

Nymphs were seen in January, but from February to April, only adults were recorded.

Truxalis viridifasciata (Krauss). (Figs 37, 38.)

Acrida (*Acridella*) *viridifasciata* Krauss, 1902 : 4.

Truxalis nasuta Burr, 1903 : 416.

Acrida viridifasciata Krauss, 1907 : 18, pl. II, figs 1, 1A.

Truxalis viridifasciata Dirsh, 1950, *Eos*, Tom. extraord., p. 196, figs 125–126.

Bio, 21 March 1953, 1 ♂ ; between R.A.F. Camp and Mahallas, limestone plateau, 26 March 1953, 1 ♂, 1 ♀ nymph ; Hadibo, 5–10 April 1953, 1 ♀ nymph.

This species was described by Krauss from Socotra, without exact locality, from a single female, which is preserved in the Vienna Museum and was redescribed by Dirsh (1950). The description of the hitherto unknown male follows :

♂.—Body moderately slender.

Antenna somewhat shorter than head and pronotum together, moderately widened at base and evenly narrowed towards apex ; all segments well separated. Fastigium of vertex with straight lateral margins and broad obtusangulate apex.

Pronotum weakly saddle-shaped ; lateral carinae in prozona sinuate, in metazona broadly divergent and incurved ; posterior angle acute, pointed ; ratio of metazona to prozona 1.5. Mesosternal interspace slightly longer than broad, with incurved lateral sides. Metasternal interspace as broad as long.

Elytron extending well beyond hind knee, with slightly convex anterior margin and acute apex; ratio of length to width, 8.

Hind femur projecting beyond the apex of abdomen. Hind knee with short acute lateral lobes, the upper lobe broader than the lower. Arolium small and narrow.

Subgenital plate in profile with straight posterior margin and subacute apex; from above, apex subconical, subacute.

General colouration greenish; lateral sides of head, lateral and median carina and lateral lobes of pronotum with pale brownish stripes. Basal disc of hind wing greenish-yellow, colour fading towards apex; the tessellate pattern brownish; apex of wing with two short dark longitudinal fasciae.

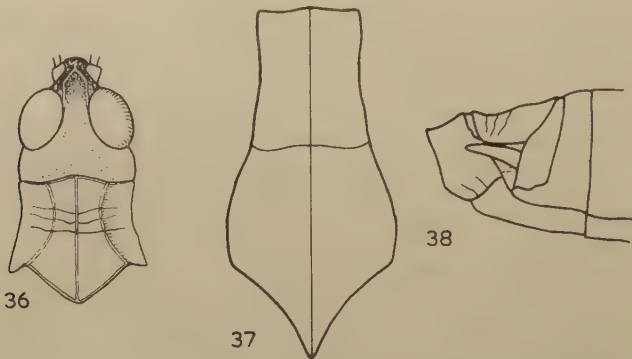


FIG. 36.—*Leva socotrana*, Popov, sp. nov., head and pronotum, ♂.

FIGS 37, 38.—*Truxalis viridifasciata* (Krauss). 37, pronotum, ♂; 38, subgenital plate, ♂.

Length of body ♂ 36 mm., ♀ 44 mm.; frons ♂ 9.5 mm., ♀ 11.0 mm.; pronotum ♂ 7 mm., ♀ 8 mm.; elytron ♂ 34.5 mm., ♀ 51.5 mm.; hind femur ♂ 23 mm., ♀ 25 mm.

Truxalis viridifasciata is closely allied to *T. conspurcata*, from which it differs by the less robust habitus, shorter head, the shape of the fastigium of vertex and the more acute elytron (Dirsh, 1950). But perhaps the most evident difference distinguishing this endemic Socotran species from all other known species of the genus, lies in the very small sexual dimorphism, the male of *T. viridifasciata* being almost as large as the female, while in all other species, the difference is much more pronounced.

Young nymphs were not uncommon on the limestone plateau in the central part of the island in March, where they occurred singly in patches of *Hyparrhaenia* and other grasses. The only two adults recorded were both captured towards the end of March, soon after the final moult.

A larva recorded by Burr (1903), as *Truxalis nasuta* (L.) was probably also *T. viridifasciata*, since *T. nasuta* is Mediterranean in its distribution (Dirsh, 1950) and its occurrence on Socotra is improbable.

Oxytruxalis ensis (Burr).

Truxalis ensis Burr, 1899 : 43.

Acerida ensis Burr, 1902. *Trans. Ent. Soc. Lond.* 2, 161.

Truxalis ensis Burr, 1903 : 416, pl. XXV, figs 4, 4a.

Oxytruxalis ensis Dirsh, 1950, *Eos*, Tom. extraord. pp. 150–151, figs 50–51.

Between R.A.F. Camp and Mahallas, 26 March 1953, 1 ♂ nymph.

No adults of this endemic genus and species were found, but the nymph recorded above undoubtedly belongs to it, as it has the characteristic shape of posterior

pronotal angle and the elongated inner lobe of the posterior knee; these characters permitted to distinguish it from nymphs of *Truxalis viridifasciata*.

THE ECOLOGY OF SOCOTRAN SALTATORIA.

A description and classification of the vegetation types found on Socotra is given by Popov in *J. Linn. Soc. (Bot.)* 55, 705, but for the present purpose a simplified grouping of vegetation was adopted.

The Lowlands.

Maritime vegetation.—The tufty salt-grass *Heleochoa dura* growing in pure stands on some coastal dunes was the only habitat in which *Ochridia kraussi* has been found: no other species of Saltatoria occurred within this vegetation.

Salt-bush communities.—The mesophilous *Pyrgomorpha cognata* was occasional here and in addition a *Thisiocetrus* sp. (similar to *Thisiocetrus rantae*) was seen but not captured within the belt of *Arthrocnemum* sp.? at Ghublet Nait between Ras Shoab and Katanahan.

Sub-desert shrub and grass.—Since the distribution of Saltatoria was mainly connected with the soil structure and the vegetation cover, rather than the floristic composition of the communities, the following subdivisions may be made on this basis and that of soil structure.

Sand belt.—The only grasshopper which could be said to favour the presence of sand, was the geophilous *Acrotylus incarnatus* but it was by no means confined to it.

Bare stone and gravel plains, with little or no vegetation cover.—The geophilous *Sphingonotus canariensis*, *S. turkanae*, *S. gangblaueri*, *Wernerella insularis*, *Scintharista forbesi* and *Acrotylus incarnatus* favoured this habitat. They have been recorded in coastal lowlands on both sides of Socotra and, with the exception of *S. canariensis*, also in the highlands. *Scintharista* was usually observed on stony and gravelly slopes and *Acrotylus* was more common on the sandier patches in the presence of small amounts of ephemeral vegetation, while the others preferred level gravelly plains.

Bare stone and gravel plains with open shrub-woody herb-short annual grass vegetation.—This was probably the most favoured of all habitats on Socotra. The preceding species still occurred within it in small numbers, but here *Caloptenopsis glaucopsis orientalis*, *Oedaleus senegalensis* and *Leva socotrana* were the commonest geophiles, together with the more phytophilous *Pyrgomorpha cognata*, *Catantops axillaris* and *Phanoptera nana*, which were usually encountered among the herbaceous vegetation. *Cyrtacanthacris tatarica* and *Anacridium melanorhodon arabafrum*, were sometimes flushed from a distance, the first from the ground and the second from shrubs, and an occasional *Physemophorus socotranus* would be seen ambling slowly along the ground, or sitting under a bush. At night, *Glomeremus pileatus* often came crawling to light and *Pachysmopoda abbreviata* and *Oecanthus chopardi* could be heard trilling in the bushes, with *Acheta rufopicta* joining the chorus from the mouth of its burrow in the ground.

Dry hill slopes with open xerophytic communities.—The population of Saltatoria in this type of habitat was rather similar to that of the open plains mentioned immediately above, but it was generally somewhat lower with the exception of *Scintharista forbesi*, which particularly favoured the stony slopes. The presence of *Oedaleus senegalensis* and *Caloptenopsis glaucopsis orientalis* was associated with the presence of short annual grasses, such as *Aristida adscensionis*, while the occasional *Truxalis viridifasciata* was recorded from patches of taller grasses, growing along the edge of dry watercourses. Other Saltatoria, such as *Dioscoridus depressus*, *Caloptenosis bimaculatus*, and *Brachytypus* spp. usually associated with denser vegetation of the next type, were also occasionally observed here.

Sub-desert shrub with trees.—The commonest species here were the geophilous *Caloptenopsis bimaculatus* and the phytophilous *Brachytypus* spp., while *Dioscoridus depressus*, *Anacridium melanorhodon*, *Pachysmopoda abbreviata* and *Oecanthus chopardi* were occasional. On the whole the population of Saltatoria in this type of habitat was low.

The Highlands (above 1000 ft.).

Bare gravelly or stony plains and slopes.—The lowland geophiles *Wernerella insularis*, *Scintharista forbesi* and *Acrotylus longipes incarnatus*, were also commonly recorded in similar habitats at a height of over 300 m. above sea-level, but were less common.

Open shrub-annual grass vegetation.—*Leva socotrana*, *Oedaleus senegalensis* and *Acrotylus incarnatus*, were dominant here, as in similar habitats in the lowlands. In taller grass, *Truxalis viridifasciata* was more common than on the coast and occurred together with the two species recorded only from the highlands—*Ermia variabilis* and *Oxytruxalis ensis*, of which *Ermia* was much more numerous. In addition, the following species were recorded as occasional: *Pachysmopoda abbreviata*, *Pyrgomorpha cognata* and *Physemophorus socotranus* and the geophilous gryllacridids, *Glomeremus capitatus* and *G. mediopictus*, both evidently confined to highlands. Generally speaking, the species enumerated above favoured the more open habitats within this type of vegetation.

Semi-arid evergreen scrub and arid sub-desert scrub.—The two types are here combined to include the thickets in the highlands, since the population of Saltatoria did not noticeably differ between them. *Caloptenopsis bimaculatus* was nearly as common in the highlands as in the lowlands and was recorded together with the generally rarer *Dioscoridus depressus* and *Anacridium melanorhodon arabafum*. Among the Eumastacidae, all three species of *Brachytypus* occurred here and *Phaulotypus granti*, which was not seen by the present collector, also apparently belongs to the same type of habitat. The single specimens of *Socotrella monstrosa* and *Thericles nanus* were both caught on the open patches of ground on the edge of thickets, but their structure and affinities would suggest a phytophilous habitat rather than a geophilous one. The single specimen of *Phaneroptila insularis* was taken from the dense undergrowth in highland thicket.

Habitats where water is present.—*Juncus arabicus* consociation. *Cataloipus brunneri*, *Homorocoryphus nitidulus* and *Conocephalus bidens* were invariably associated with this community, but the last two were rare on the coast. The more mesophilous *Aiolopus thalassinus* was also frequently found in this habitat.

Moist sand along banks of streams in the presence of semi-aquatic vegetation.—*Paratettix* sp. was locally common in this type of habitat at Hadibo. *Gryllotalpa africana* also chose it for digging its burrow and was recorded wherever it occurred on Socotra.

River banks with cultivations and/or scrub vegetation.—This appeared to be the favourite habitat of the mesophilous *Catantops axillaris*, *Pyrgomorpha cognata*, phytophilous *Aiolopus thalassinus* and geophilous *Acrotylus incarnatus*.

General Remarks.

Only few generalizations emerge from the above.

The distribution of geophiles appears to be not so much dependent on the geological or chemical characteristics of the soil, as on its surface. Thus, species common to stony scree, are usually found on such scree, whether they are of granite, basalt or limestone, but appear to avoid rocky or sandy slopes. On Socotra geophiles were well represented and occurred in all parts of the island, so long as open patches of the appropriate soil structure were present. On the whole, this group was more common

in the coastal areas, but with the exception of *Sphingonotus canariensis*, all species were also recorded from the highlands.

The choice of the habitat by phytophiles is apparently also governed by the structure of the vegetation rather than its floristic composition. Thus, among the grassland Acrididae, it is possible to differentiate between those of the tall grass and the short grass, but the species of the grass is of secondary importance. Preference for a particular plant may be shown in the sense that the insect is more often associated with it than any other species of plant, but the range of the insect is usually found to differ from that of the favoured plant and alternative species are acceptable. An example of this on Socotra is given by the frequently observed association of *Brachytypus socotranus* with *Jatropha unicostata*, but the range of this Eumastacid was found to be greater than that of the plant. Another case of even closer apparent dependence on a single host plant was that of the several species of Saltatoria (*Cataloipus*, *Conocephalus*, *Homorocoryphus*) found only on *Juncus arabicus*. The explanation, suggested by the habitat requirements of the same or allied species elsewhere, is that on Socotra *Juncus* consociation is the nearest approach to a tall grass community with which these insects are associated elsewhere. Similar explanation can also be suggested for the occurrence of *Ochridia* only on *Heleochloa dura*.

ZOOGEOGRAPHICAL CONSIDERATIONS.

The most striking feature of the Socotran fauna of Saltatoria is a very high degree of endemism (see table). No less than 26 out of the total 41 species (63 per cent) and 8 out of 34 genera (24 per cent) are restricted to the island; in addition, one of the genera constitutes an endemic subfamily Socotrellinae.

The 15 non-endemic species are all good fliers and practically all have a wide distribution, extending, at least, over the Eremian region in Africa and Asia, and in several cases well beyond it, mostly into tropical Africa.

The fact that in some cases (*Anacridium melanorhodon arabafum*, *Caloptenopsis glaucopsis orientalis*) there is even no subspecific differentiation from the forms occurring in Africa and Arabia suggests that the non-endemic species are either geologically very recent arrivals to Socotra, or even that there is a frequent exchange of populations of these highly mobile insects between the island and the adjoining mainlands. These species, therefore, are of little value for a discussion of faunistic affinities, except that even in their case there is a clear indication that the Socotran fauna includes no elements which could be considered of truly Palaearctic and even of Mediterranean origin, while it has close affinities with the fauna of arid and semi-arid parts of subtropical Africa.

As regards the endemic element, the affinities of the endemic species of more widely distributed genera lie also in the same direction. The genera *Conocephalus*, *Oecanthus* and *Achaeta* are very widely distributed in the tropics and subtropics of both hemispheres; some species penetrate into the temperate zone, but the tropical origin of the genera is unquestionable. *Caloptenopsis*, *Cataloipus* and *Truxalis* are genera of rather wide distribution in subtropical grasslands of Africa and southern Asia, with some species just penetrating northwards into semi-deserts. *Glomeremus* and *Clerithes* are essentially African genera, while *Ermia*, although known only from Socotra and Somaliland, is a member of the *Ochridia* group of genera which is predominantly African and Eremian. The genus *Sphingonotus*, represented on Socotra by two widely spread Eremian species and an endemic one, belongs to an ancient Eremian element and has a discontinuous distribution in the desert areas of North and South Africa and Asia, with isolated species in the Western Hemisphere. The case of *Wernerella* is similar, as it occurs discontinuously in the Canary Islands Morocco and South Africa, while *Scintharista* is, in addition, represented in semi-deserts of south-western Asia. Thus, on the whole, the genera which include endemic

Socotran species exhibit the same tropical Ethiopian and Eremian affinities as the non-endemic species.

The eight genera endemic to Socotra conform to the same biogeographical pattern. The genera *Brachytypus*, *Phaulotypus* and *Oxytruxalis* are clearly derivable from the allied genera of the African savannas, while *Dioscoridus* and *Physemophorus* may be regarded as members of the same fauna, particularly adapted to life on trees and shrubs. *Pachysmopoda* and *Phaneroptila* have affinities with some genera of wide distribution in the Old World tropics, while *Socotrella* belongs to an endemic subfamily of the family Eumastacidae with world-wide tropical distribution.

The above analysis makes it clear that the Socotran fauna of Saltatoria has been essentially derived from the Ethiopian one, and particularly from its more xerophilous

Distribution of Socotran Saltatoria.

	Endemic		Africa	Arabia	Other
	Genus	Species			
<i>Glomeremus pileatus</i>	..	+	
<i>capitatus</i>	..	+	
<i>mediopictus</i>	..	+	
<i>Pachysmopoda abbreviata</i>	+	+	
<i>Phaneroptera nana</i>	+	+	
<i>Phaneroptila insularis</i>	+	+	
<i>Conocephalus bidens</i>	..	+	
<i>Homorocoryphus nitidulus</i>	+	+	SW. Asia, S. Europe.
<i>Oecanthus chopardi</i>	..	+	
<i>Achaeta rufopicta</i>	..	+	
<i>Gryllotalpa africana</i>	+	+	Old World Tropics.
<i>Brachytypus insularis</i>	+	+	
<i>socotranus</i>	..	+	
<i>dioscoridus</i>	..	+	
<i>Phaulotypus granti</i>	+	+	
<i>Clerithes</i> (?) <i>namus</i>	..	+	
<i>Socotrella monstrosa</i>	+	+	
<i>Pyrgomorpha cognata</i>	+	+	Eremian region.
<i>Physemophorus socotranus</i>	+	+	
<i>Catantops axillaris</i>	+	+	S. Persia.
<i>Caloptenopsis</i>					
<i>glaucoptis orientalis</i>	+	+	
<i>bimaculatus</i>	..	+	
<i>Dioscoridus depressus</i>	+	+	
<i>Cataloipus brunneri</i>	..	+	
<i>Thisoicetrus caeruleus</i>	+	+	
<i>Schistocerca gregaria</i>	+	+	Eremian region.
<i>Anacridium melanorhodon</i>					
<i>arabafum</i>	+	+	
<i>Cyrtacanthacris tatarica</i>	+	+	S. Asia.
<i>Sphingonotus canariensis</i>	+	+	Eremian region.
<i>turkanae</i>	+	+	" "
<i>ganglbaueri</i>	..	+	
<i>Wernerella insularis</i>	..	+	
<i>Acrotylus incarnatus</i>	..	+	+	..	
<i>Oedaleus senegalensis</i>	+	+	Eremian region.
<i>Scintharista forbesi</i>	..	+	
<i>Aiolopus thalassinus</i>	+	+	Europe, Asia.
<i>Ochridia kraussi</i>	+	+	Eremian region.
<i>Ermia variabilis</i>	..	+	
<i>Leva socotrana</i>	..	+	
<i>Truxalis viridifasciata</i>	..	+	
<i>Oxytruxalis ensis</i>	+	+	

component, while no Palaearctic influence can be discerned in its composition. This conclusion may appear very different from that reached by Parker (*The Snakes of Somaliland and the Socotra Islands*. Leiden, 1949), who regarded the snakes of Socotra as being more closely related to the Palaearctic and Oriental than to the Ethiopian fauna. The difference, however, is due only to differing conceptions of Palaearctic fauna. Parker includes in the Palaearctic region the so-called, Saharo-Sindian area which other authors and I regard as a part of the Eremian region. Parker's conclusion is based on four species of snakes, three of which are endemic to Socotra and one, doubtfully recorded from the island, is classified as Saharo-Sindian. One of the endemic species (*Typhlops socotranus*) "belongs to a cosmopolitan genus but would appear to be most closely related to a Palaearctic species"; the second (*Coluber socotrae*) is regarded (*t.c.*, p. 5) as "primitive species of a Palaearctic-Nearctic genus", but the *florulentus* group, to which it is stated to be most closely related, appears to be rather well represented in north-east Africa; the third (*Dityophis vivax*) "appears to have Oriental as well as African affinities". Therefore, if one considers the Eremian fauna as distinct from the Palaearctic, the snake fauna of Socotra provides support for my conclusions regarding its Saltatorian fauna. Indeed, this seems to be also Parker's final conclusion, since he says (*t.c.*, p. 14) that the "fauna of Socotra consists of changed and unchanged survivors from the mid-Pliocene fauna of the north-east corner of Africa which he regarded (*t.c.*, p. 9) as "predominantly Ethiopian".

The high degree of endemism of the Socotran fauna suggests its long isolation from the mainlands of Africa and Arabia. The fact that there are no subspecies endemic to Socotra, suggests that the isolation occurred at a sufficiently remote period to allow some 63 per cent of its fauna to become differentiated at the specific level. Even more significant is the presence of eight endemic genera and of one endemic subfamily. There is, of course, no palaeontological evidence on the possible age of the endemic elements and any attempt to estimate the age by reference to the geological history of the island (which itself is very imperfectly established) can only be a speculation. It is possible, however, to suggest that some of the endemic species and genera are relics of a very ancient fauna surviving mainly in the Hagghier massif which geologists consider not to have been submerged since the Mesozoic at least. The separation of Socotra from the African mainland is believed to have occurred in the middle of Pliocene (Arlt, 1919). The endemic Socotran Saltatoria, therefore, may be reasonably suggested to represent relics of the Tertiary fauna of the African continent which survived on the island without being much affected by the more recent developments of the Ethiopian fauna. The last statement is based on the fact, established above, that the few species common to Africa and Socotra are good fliers and would be able to reach the island across the sea, while most of the endemics are either flightless or, apparently, poor fliers.

One of the Socotran endemic species, *Ermia variabilis* presents a very interesting case of extremely wide variability in several morphological characters (see p. 381). Some of these characters are usually sufficiently stable to be used as specific criteria in this group, but in *E. variabilis* variations in structure are found in the same populations and suggest genetic instability of the species. A similar remark might be made about *Leva socotrana* (p. 382) but its range of variation is not greater than in some other species of the genus.

ON OPISTHOBRANCHIA FROM BRAZIL (2)*. By ERNESTO MARCUS,
F.M.L.S., University of S. Paulo, Brazil.

(With Figures 1-246.)

[Read 24 May, 1957.]

The term Opisthobranchia is here used in its popular sense, to mean Gastropoda Euthyneura excluding the former Orders Pteropoda and Pulmonata.

Mrs. EVELINE DU BOIS-REYMOND MARCUS and I try to record the Opisthobranchia of the upper littoral of Brazil in order to prepare the way for studies like those of T. J. Evans, J. E. Forrest, V. Fretter, A. Graham and others. Work of this kind explains the phenomena of life and puts in evidence similarities between different systematic units. These resemblances may be due to convergence or may be true homologies, the classical object of morphology (Remane, 1954).

In this last and very important branch of malacology we are beginners and therefore follow the system of Odhner (1939) closely. Only we want to maintain the idea of the Tectibranchia, in the restricted sense of Thiele's Pleurocoela (1931), for Cephalaspidea and Anaspidea. A study of *Cylindrobulla* (Marcus, 1956) showed us the relations between the cephalaspidean *Cylindrobulla* and the Akeridae which connect Cephalaspidea and Anaspidea.

If we now present a less incomplete bibliography than in our preceding paper, we owe it principally to the many colleagues who kindly sent us their publications. We cannot thank them all one by one here, but want to mention Professor Dr. C. R. Boettger (Braunschweig) for his expert help and Dr. S. A. Gerlach (Kiel) for the photocopy of Bergh's *Malacologische Untersuchungen*, a work of more than 2,000 pages and plates. My sincere thanks are due to Professor Alastair Graham for his careful correction of the language.

Hoffmann (1932-40) has extracted innumerable morphological details from Bergh and synthesised them with incomparable ability. Thiele's treatise gave a summary of Bergh's systematic results. Nevertheless the laborious study of Bergh's papers is indispensable, in as much as the taxonomically important reproductive organs are not treated in Bronn.

We are grateful to the National Research Council (Conselho Nacional de Pesquisas), Rio de Janeiro, for a contribution to the expenses of our collecting trips.

List of species discussed in the present paper :

TECTIBRANCHIA

CEPHALASPIDEA

BULLIDAE

Bulla striata Bruguière.

ATYIDAE

Haminoea elegans (Gray).

SACOGLOSSA

OXYNOACEA

OXYNOIDAE

Lobiger (Lobiger) souverbiei P. Fischer.

ELYSIACEA

HERMAEIDAE

Stiliger vanellus sp. nov.

ELYSIIDAE

Elysia cauze sp. nov.

Elysia evelinae sp. nov.

NOTASPIDEA

PLEUROBRANCHACEA

PLEUROBRANCHIDAE

Berthella tupala sp. nov.

* Opisthobranchia from Brazil (1), see *Bol. Fac. Fil. Ci. Letr. Univ. S. Paulo*, Zoologia No. 20, 1955.

NUDIBRANCHIA

DORIDACEA-EUDORIDACEA

CRYPTOBRANCHIA

DORIDIDAE

GLOSSODORIDINAE

Glossodoris neona Marcus.*Hallaxa aepae* sp. nov.

DORIDINAE

Doris verrucosa Cuvier.

PLATYDORIDINAE

Platydoris angustipes (Mörch).

PHANEROBRANCHIA

NONSUCTORIA

POLYCERIDAE

Thecacera pennigera (Montagu).*Polycerella conyna* sp. nov.*Polycera aurisula* sp. nov.

SUCTORIA

GONIODORIDIDAE

Okenia impexa sp. nov.*Okenia evelinae* sp. nov.*Trapania maringa* sp. nov.

DORIDACEA-POROSTOMATA

DENDRODORIDAE

Dendodoris atropos (Bergh).

DENDRONOTACEA

LOMANOTIDAE

Lomanotus phiops sp. nov.

HANCOCKIIDAE

Hancockia ryrca sp. nov.

DOTONIDAE

Doto pita Marcus.*Doto uva* Marcus.*Doto caramella* sp. nov.

EOLIDACEA

ACLEIOPROCTA

CUTHONIDAE

CUTHONINAE

Catriona tina sp. nov.

TERGIPEDINAE

Tergipes despectus (Johnston).*Embletonia evelinae* sp. nov.

CLEIOPROCTA

FACELINIDAE

FACELININAE

Phidiana selenkai Bergh.

FAVORININAE

Cratena kaoruae sp. nov.*Nanuca sebastiani* gen. et sp. nov.

SPURILLIDAE

Spurilla neapolitana var. *braziliana*

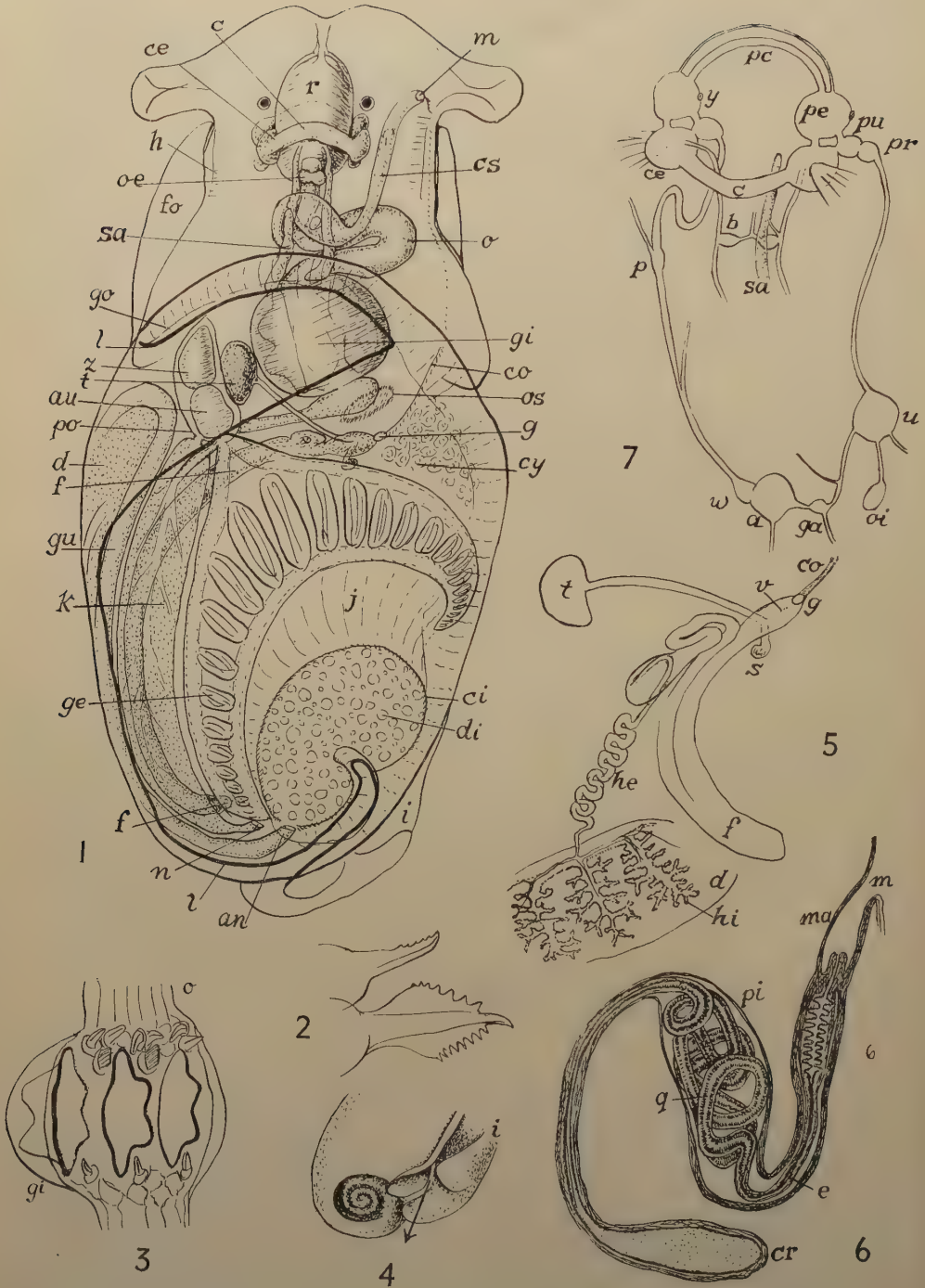
MacFarland.

Berghia coerulescens (Laurillard).

Specimens and slides are deposited in the Department of Zoology, Faculty of Philosophy of the University of S. Paulo (Brazil).

Anatomical Notes on *Bulla striata* Brug. (Figs 1-8.)

Though Risbec (1951, p. 113) considers the anatomy of *Bulla* as rather well known, looking through Bronn one notes numerous gaps. The older anatomical studies, e.g. of Vayssière (1885) and Bergh (1901), refer principally to the cuticular elements of the alimentary tract. The small differences between the Mediterranean snails (Vayssière) and those from the Virgin Islands (Bergh) are not sufficient for specific separation. A preparation of the roof of the pallial cavity (Köhler, 1893, pl. 4, fig. 60) and Guiart's diagram of the nervous system (1901, fig. 76) were reproduced in Bronn (figs. 194, 584C). Tchang Si's valuable dissertation (1931) remained little known, but Pruvot-Fol (1954, fig. 5) reproduces Si's principal drawing of the anatomy



of *B. striata*. The nervous system of the Indian *B. ampulla* L. (Eales, 1938, p. 81) agrees with that of *B. striata*.

We obtained many living snails on the coast of the island of S. Sebastião in the first half of November 1955, in very shallow water near the mouth of the River Perequê, in muddy sand above the low-water line. Oliveira & Krau (1953, p. 524) found living snails in the Bay of Rio under similar conditions, while d'Orbigny (1837, p. 213), also in Rio, obtained them only well below the lowest spring tides. In the neighbourhood of Toulon (Si, 1931, pp. 15-16, 29, 40-41) *B. striata* hides in the mud during the day, creeps out at night and, in the aquarium, spawns at about 5 o'clock in the morning. On the coast Si found the egg clusters in shallow water. The only spawn that we found was a club-shaped structure, about 2 cm. long and up to 0.8 mm. in diameter. The narrow handle of the club was fixed to a stone. As an adult snail was caught near this stone in the sand, we are convinced that it had produced the spawn. Si (1931, pp. 40-42) described a very different egg mass. Perhaps our snail had only begun to lay its eggs, so that its spawn corresponds to a small part of a normal cluster.

One shell of our new collection is larger than the largest of the 150 previously measured (Marcus, 1955), viz. 39 mm. long and 22.7 mm. in greatest diameter. Our smallest shell was 1.1 mm. long and 0.76 mm. broad. This snail was found among algae. Its radula (Fig. 2) consists of about 8 rows, the median tooth has 9 denticles, the inner lateral tooth is 42 micra high, the outer lateral 28 micra. Both differ in shape from the corresponding adult teeth. Marginal teeth are not developed in this young radula. A snail with a shell about 28 mm. long had 25 rows of radula teeth, the older half of which was brownish. The two oldest rhachidian teeth were so worn that they had no denticles at all. The mandibles and the gizzard plates of the new material are like the older descriptions. The mandibles are more or less semicircular, about 1.5 mm. long, 1 mm. broad and built up by closely-packed columns. Before and behind the big gizzard plates, papillae with spines and plates occur (Fig. 3), the number of which varies even in the three sectors of the same gizzard. In fresh material the aspect of the three big plates is somewhat different from our previous figures. Their orange, horny, more or less smooth surface is directed inwards and has broad black edges, while the basal knob of cartilaginous consistency is implanted in the musculature.

FIGURES 1-7.

Bulla striata Bruguière. (Figs 1-7.)

FIG. 1.—Diagram of organization.

FIG. 2.—Lateral radular teeth of young snail (shell 1.1 mm. long).

FIG. 3.—Opened gizzard.

FIG. 4.—Hind end without shell.

FIG. 5.—Reproductive organs.

FIG. 6.—Male copulatory organ.

FIG. 7.—Nervous system, slightly distorted by compression.

a—abdominal ganglion. *an*—anus. *au*—auricle of heart. *b*—buccal ganglion. *c*—cerebral commissure. *ce*—cerebral ganglion. *ci*—ciliated bands. *cm*—columellar muscle. *co*—ciliated groove. *cr*—root of penis. *cs*—male copulatory organ. *cy*—crypt-like glands. *d*—digestive gland. *di*—discoidal gland. *e*—ectal part of ejaculatory duct. *f*—female gland mass. *fo*—foot. *g*—genital aperture. *ga*—genital ganglion. *ge*—gill. *gi*—gizzard. *go*—glands of mantle border. *gu*—intestine. *h*—Hancock's organ. *he*—hermaphrodite duct. *hi*—hermaphrodite gland. *i*—infrapallial lobe. *j*—hypobranchial gland. *k*—kidney. *l*—limit of mantle cavity. *m*—male opening. *ma*—male vestibulum. *n*—renal pore. *o*—oesophagus. *oe*—oesophageal diverticulum. *oi*—osphradial ganglion. *os*—osphradium. *p*—left parietal ganglion. *pc*—pedal and parapedal commissure. *pe*—pedal ganglion. *pi*—penial sheath. *po*—pericardium. *pr*—right parietal ganglion. *pu*—right pleural ganglion. *q*—prostatic part of ejaculatory duct. *r*—pharynx. *s*—spermatocyst. *sa*—salivary gland. *t*—spermatheca. *u*—supra-intestinal ganglion. *v*—vaginal groove. *w*—sub-intestinal ganglion. *x*—shell-forming glands. *y*—statocyst. *z*—ventricle of heart.

The dorsal oesophageal diverticulum discovered by Pelseneer was questioned by Hoffmann (1938, p. 1077). It was however confirmed by Si (1931, pp. 34-35: "poche de Pelseneer") and occurs in our material too (*oe*).

The food consists of seaweeds and along with these, sand and material of animal origin, e.g. sponges, are consumed occasionally. Si (1931, p. 146) calls *B. striata* omnivorous.

The mantle cavity opens along the whole length of the right side. The thickened dorsal (left) and the bilobed ventral (right, *i*) edge of the mantle skirt unite at the hind end and project with an exhalant siphon (Fretter & Graham, 1954, p. 567) from under the vertex of the shell. The anus (*an*) occupies, as in *Acteon* (loc. cit., p. 578), the innermost part of the pallial cavity. It lies on a salient papilla in one of our dissected animals and in the furrow between roof and floor of the mantle cavity in the others. The renal pore (*n*) is located left of the anus. Dorsal and ventral to the latter are ciliated bands (*ci*) that run in a curve to the right side and extend to near the edge of the mantle skirt. The dorsal band lies in a groove, the ventral one on a ridge. The long cilia evidently drive the faeces out of the exhalant siphon. This action is facilitated by thick white mucus produced by voluminous glands (*di*) in the floor and the roof of the pallial cavity. Together they form the discoidal gland (Hoffmann, 1933, p. 300); it occupies the field surrounded by the ciliated curves, continuing from the roof to the floor of the cavity.

No pallial caecum enters the spire, but only the liver (*d*), the hermaphrodite gland (*hi*) and a blood sinus. The ciliated bands end where the dorsal and ventral mantle skirt meet. In one snail the glands of the mantle skirt (*go*) show as white balls in the left half of the anterior edge, in the others these glands only thicken the corresponding region. Behind the gill (*ge*) the well developed mucous hypobranchial gland (*j*) lies dorsally. More or less distinct in the dozen snails that were dissected are the glands (*cy*) in front of the genital opening (*g*), on the floor of the pallial cavity. Where they are fully developed, their crypt-like structure (Hoffmann, 1934, p. 336) is striking.

The osphradium (*os*) is situated on the roof of the cavity near the anterior end of its aperture. The enormous gill (*ge*) and the heart, with the auricle posterior to the ventricle (*au*, *z*), were correctly drawn by Si (1931, fig. 1). The kidney (*k*) is located in the roof of the pallial cavity, and its anterior right end communicates with the pericardium (*po*).

The yellowish-brown hermaphrodite gland (*hi*) (Fig. 5) interdigitates with the green digestive gland (*d*). The gonad is a ramified tube, the branches of which are intermingled with blood spaces. The multiple efferent ductules unite to form the coiled hermaphrodite duct (*he*), the silky aspect of which is due to masses of sperm. A distal loop of the duct is narrow.

The mucus gland (*f*) is a very long and folded tube. It runs parallel to the gut and encloses the winding albumen gland in its distal course. The following outermost part lodges a ciliated furrow (*v*) that extends from the common genital aperture (*g*) inwards. This ciliated gutter functions as a vagina and communicates with two spherical seminal vesicles by diverging canals. The short canal leads to a small spermatocyst (*s*) that neither Si (1931) nor Risbec (1951) observed. A very long canal goes to a big spermatheca (*t*) which is filled with brown contents. The spermathecal duct runs close to the floor of the pallial cavity and dorsal to the alimentary tract (Si, 1931, fig. 1, *Vs*), while Risbec (1951, fig. 9) let it pass ventrally in *Bulla ampulla* L. Proximally the spermathecal canal of *B. striata* bends towards the pallial roof, and the vesicle lies to the right and in front of the heart. Possibly the brownish "blood gland" of Bergh's description (1901, p. 220) is the spermatheca; we did not find a special blood gland.

The external seminal groove (*co*) runs from the common genital aperture (*g*) to the opening (*m*) of the male vestibulum located in front of the right Hancock's organ (*h*). There is no continuation of the seminal groove along the inner side of the vestibulum (*ma*) as in *Aplysia* (Eales, 1921, pp. 62-63, pl. 6, fig. 19, *sem. gr.*) nor

is the penis grooved for conducting the sperm. A canal that leads the sperm from the seminal groove through the body cavity to the root of the penis (*cr*) (Fig. 6) as in *Philine* and *Cylindrobulla* is not present.

The male copulatory organ (*cs*) is a blind epithelial tube or an ejaculatory duct with a muscular wall. The innermost part is wide (*cr*) and serves as seminal vesicle. It does not agree with Vayssière's description of the terminal region of the penis of *Bulla ampulla* (1906, p. 20, pl. 2, fig. 29). In the following section a thin muscular sheath (*pi*) involves the closely-coiled duct, the epithelium of which is high and glandular (*g*). If any part is to be called prostatic it is this and not the inner caecum (Si, 1931, p. 36). External to the coiled portion of the copulatory organ the muscular sheath thickens (*e*) and the epithelium is thrust into folds. Then the inner and outer muscular layers unite and the duct forms a papilla that projects more or less into the male vestibulum (*ma*).

Spermatozoa must enter the copulatory organ from its outer end. Perhaps this is brought about by a sucking action of the basal penial bulb (*cr*).

The nervous system of *Bulla* is pleuroneural and slightly aponotoneural (Hoffmann, 1936, pp. 852-853). A vestige of torsion is indicated by the more ventral subintestinal ganglion (*w*) (Fig. 7) and the more dorsal supra-intestinal one (*u*). The nerve ring runs around the anterior end of the pharyngeal bulb (*r*) (Fig. 1) in contracted snails, while it lies behind its middle on extension. The pedal (and parapedal) and cerebral commissures (*pc*, *c*) are very long. The cerebropedal, pleuropedal and the short cerebropleural connectives are distinct. The pedal ganglia (*pe*) are as voluminous as the cerebral (*ce*) and lie in front of the latter as in *B. ampulla* (Eales, 1938, fig. 2). The right parietal ganglion (*pr*) adjoins the corresponding pleural ganglion (*pu*), the left (*p*) lies near the middle of the pleuro-subintestinal connective. The supra-intestinal ganglion (*u*) is voluminous, the subintestinal one (*w*) is connected with the big abdominal ganglion (*a*). Near the last lies an accessory genital ganglion (*ga*). The so-called buccal ganglia (*b*), perhaps better bulbo-oesophageal ganglia (Si, 1931, p. 40), certainly follow the movement of the pharynx forwards, when the snail feeds. Eales (1938, p. 82) assumes that even the long cerebrobuccal connectives are carried through the nerve ring.

The nervous system of *Bulla* is similar to that of *Haminoea* (Athyidae) though a little less concentrated. *Newnesia antarctica* Smith of the Diaphanidae has a nervous system (Odhner, 1926, fig. 6) very similar to that of *Bulla*, especially when a fusion of the right parietal with the right pleural ganglion is admitted (Hoffmann, 1936, p. 652). *Haminoea* and *Newnesia* however show a more pronounced telencephalization (Wirz, 1952, p. 172) than *Bulla*, where not only are the pedal ganglia as big as the cerebral, but also the supra-intestinal and the abdominal ganglion each attain the size of one of the cerebral ganglia. *Acteon* and *Cylindrobulla* are much more telencephalized than *Bulla*, and their visceral loop is more primitive.

Haminoea elegans (Gray). (Figs 9-16.)

This species is represented by about 100 shells thrown on to the beach, where they were distributed quite irregularly. About half of them contained the dried soft parts.

The thin shell is ovoid, broadest near the middle and forms one-and-a-half whorls. The apex is truncate with a sunken and narrowly-perforated spire. The outer lip rises from the left side of the perforation, overtops the apex, is rounded above and below, and sharp. The columella is deeply concave; its crescent-shaped, reflected white margin varies in breadth and thickness. The upper part of the inner lip is coated with a thin layer of pearly enamel that can be confluent with the reflected columellar border below and encircle the apical depression. The latter is rounded, not carinate.

The shell is subpellucid, sufficiently transparent to show the superficial structure from the inside. The growth lines are equally distinct from the apex to the columella. There are about 70 simple spiral striae closely but somewhat irregularly interspaced. They are straight, but are sometimes made slightly wavy by the axial sculpture, and are visible with the naked eye.

The colour of the silky-looking shell varies from whitish or ivory to yellow, horny brown, reddish, purplish and sometimes greenish-grey. Larger specimens are generally darker. The colour is located in the periostracum and is denser in the spiral striae. The brilliant inner side has the same colour as the outer surface. The fleshy parts, which were only seen in the dried state, are dotted with black.

Greatest diameter and total length were measured in 60 shells that varied in length from 23.5 to 13.5 mm. and in greatest diameter from 16.5 to 9.5 mm. The ratio greatest diameter to length varied from 1 : 1.28 to 1 : 1.56, the mean being 1 : 1.42.

As the shell in young and old snails always forms one-and-a-half whorls, we conclude that it is dissolved in the centre while it grows on the outside. This fact explains the absence of a larval shell.

The jaws (Fig. 12) are semicircular plates consisting of stratified rodlets which are longer in the centre than near the margin. Also the cuticle between the jaws has a reticular sculpture. The radula is 1.95 mm. long and 1.4 mm. broad. Its formula is $35-39 \times 20, 1, 20$. The number of teeth is the same in five snails which were examined, the shells of which were about 20 mm. in length. In all of them the rhachidian teeth have a rough, nearly hairy base. The lateral teeth are generally quite smooth; sometimes the two inner have a very slight outer folding at the point where the hook begins, but not the saw of denticles of *H. hydatina* (L.) as figured by Thiele (1931, fig. 485, p. 386). The proportions of the first lateral tooth are very variable: in one radula its cusp is 85 micra long and 36 micra broad, while the corresponding measurements are 62 and 42 micra in another radula (Fig. 13). In both cases the cusp of the fifth lateral tooth is 100 micra long and 28 micra broad.

The three big gizzard plates (Fig. 14), each comparable with a many-valved chiton (Schepman, 1913, p. 474) have about twenty-four ridges. These lie on the same level on both sides of the median crest or alternate. The biggest plates are 2 mm. long and 1.6 mm. broad.

Occurrence : Island of São Sebastião on the beach, 10-20 April 1954.

Further distribution : Rio de Janeiro; West Indies; from the west coast of Florida to Texas.

FIGURES 8-16.

Bulla striata Bruguière. (Fig. 8.)

FIG. 8.—Transverse section near hind end.

ci—ciliated bands. *cm*—columellar muscle. *d*—digestive gland. *di*—discoidal gland. *gu*—intestine. *i*—infrapallial lobe. *j*—hypobranchial gland. *k*—kidney. *l*—limit of mantle cavity. *x*—shell-forming glands.

Haminoea elegans (Gray). (Figs 9-16.)

FIG. 9.—Shell, ventral view.

FIG. 10.—Shell from apex.

FIG. 11.—Shell from below.

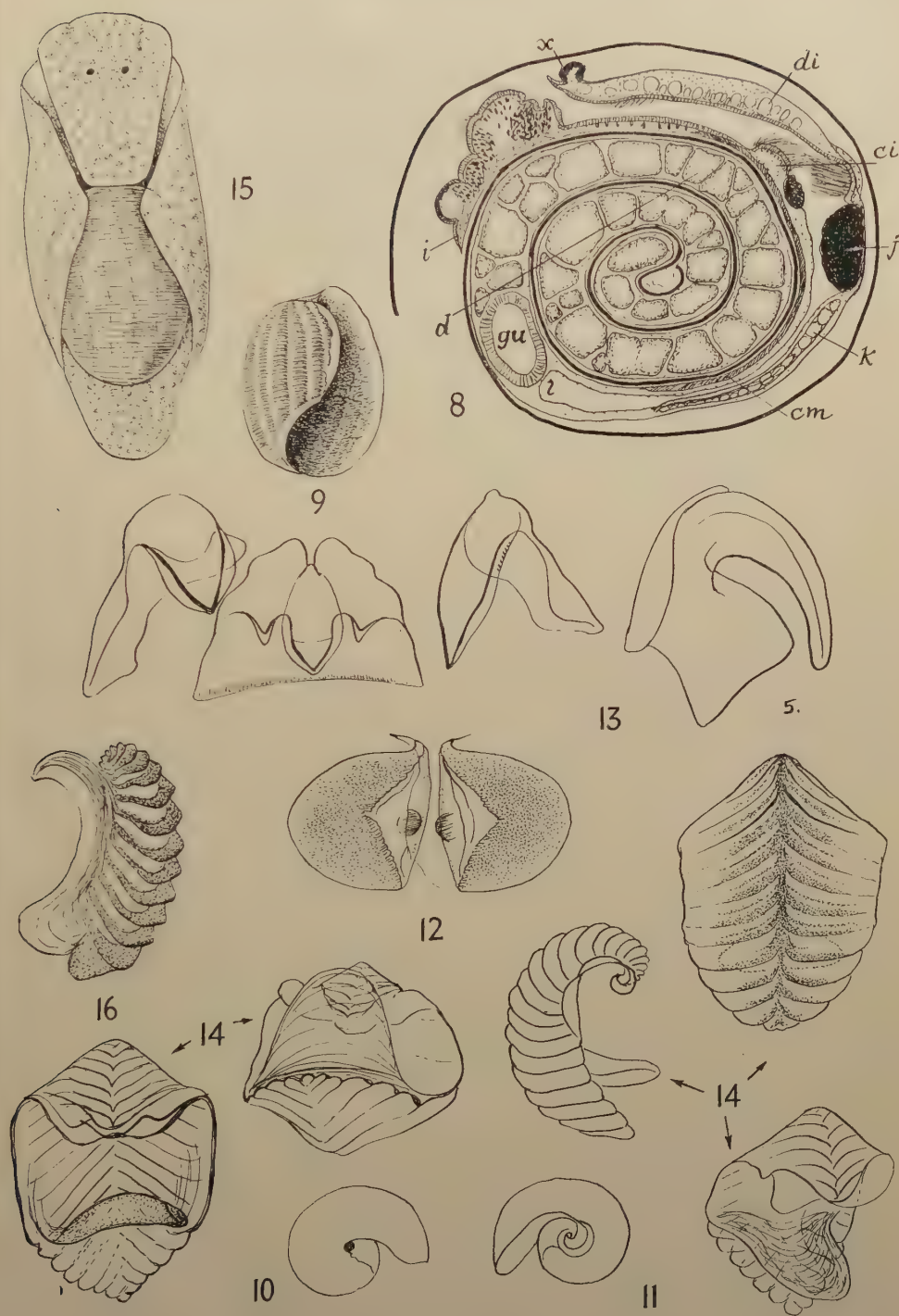
FIG. 12.—Jaw plates.

FIG. 13.—Rhachidian, first lateral and fifth lateral tooth from one, and first lateral tooth from another specimen.

FIG. 14.—Gizzard plates in different views.

FIG. 15.—Living snail, 10 mm. long.

FIG. 16.—Gizzard plate of same.



Notes on young *Haminoea elegans*.

Four young snails were found among algae in the upper littoral of the island of São Sebastião; and 14 km. west of Ubatuba. There was no correlation between their size from 2.5 to 10 mm. alive and the months in which they were caught, July, September, and November. The shell of the smallest snail was 1.8 mm. long and 1.3 mm. broad. The three smallest snails have closely-set red dots in their tissue, especially in the mantle. The fundamental colour of all four is greyish green; the biggest had black pigment spots (Fig. 15). The head shield of the youngest snail is bilobed, while its posterior border is entire in the largest. The radula of the smallest specimen consists of sixteen rows; the most anterior, first developed row has the formula 4, 1, 4. There is no pre-radula in this animal. Its first lateral teeth have a denticulated outer edge that was not observed in the adult nor in the bigger young animals. The gizzard plates have nine ridges and are 0.27 mm. long in the youngest snail. The six small teeth that lie in front of and between the gizzard plates are each split up into a tuft of fibres in this particular group of young animals after treatment with KOH. We could not compare them with the teeth of the adult, in the dried flesh of which they were not found. The organ of Hancock was composed of sixteen pairs of leaves in the 10 mm. long snail.

At 24° C. the heart of the 2.5 mm. long snail beat 160 times in a minute.

Discussion of *Haminoea elegans*.

We consider our material as specifically identical with *Bulla diaphana* Gould (1852, p. 222, pl. 15, figs. 265, 265a-d) from Rio de Janeiro. Gould, indeed mentioned the resemblance of his species to *elegans*. Pilsbry (1893, p. 356) tentatively united *diaphana* and *elegans* and included Rio de Janeiro in the distribution of *elegans*. Kobelt (1896, p. 101) used the name *Haminea guildingii* (Swainson) 1840 (see Reeve, 1868, pl. 1, figs. 5a, b), but after Dall (1889, p. 57), Pilsbry (1893, p. 356), and Dall & Simpson (1901, p. 361) *guildingii* must be united with *elegans*. Thereafter the literature on Brazilian Opisthobranchia (MacFarland, 1909, p. 8; Ihering, 1915, p. 138; Lange de Morretes, 1949, p. 113) called the species *Haminoea elegans* (Gray), 1825.

Lemche (1948, pp. 88-89) unites the West Atlantic species with the European *hydatis* (L.) and *navicula* (da Costa, 1778) without deciding whether these two are varieties or separate species. Pilsbry (1893, p. 356) is strictly against the union of Gray's species with any of the European, and we do not feel authorized to contradict his opinion. After Bergh's examination (1900, p. 160; 1901, p. 222) of *H. cornea* (Lamarck 1822 = *navicula* da Costa) and *H. hydatis* their identity seemed to be established (Vayssi re, 1913, p. 164). Later on, Si (1931, pp. 42, 50), Vayssi re (1932, *Faune & Flore M d.*) and Pruvot-Fol (1954, pp. 79, 81) separated them again.

If this separation prevails, *elegans* is less distant from *navicula* than from *hydatis*. The more or less bilobed posterior border of the cephalic shield and denticulated edges of the first to third lateral teeth of the radula (Guiart, 1901, figs. 33, 34) have evidently no taxonomic value.

Lobiger souverbiei P. Fischer. (Figs 17-29.)

Lobiger Souverbii P. Fischer, 1856, p. 273, pl. 11, figs. 7-10.

Lobiger (Dipterophysis) souverbii Pilsbry, 1896, p. 168, pl. 10, figs. 39-42.

Lobiger souverbiei Engel, 1927, p. 112, fig. 28.

The living snail was about 20 mm. long; preserved it is 11 mm. The whole body is light green, and this colour also shines through the transparent shell. The skin bears the following pigment marks: (1) Six thin, black, longitudinal strokes under the shell, two of which are about one-third shorter than the others (Fig. 17) These strokes are edged with yellow, and the three longest of them include some light

blue dots. The blue effect is brought about by an occasionally deeper course of the black stroke that is covered by the white epidermis on these spots. (2) Small brown superficial chromatophores in the skin of the head, on the outer side of the rhinophores, on the dorsal surface of the foot, the border of the mantle and on the under surface of the parapodial lobes. Here the pigment cells are concentrated around the warts and along the borders. They are, however, not the "thick flask-shaped chromatophores" (Si. 1931, p. 85, pl. 6, fig. 2, c) of *L. serradifalci* (Calc.) which are cutaneous glands. (3) The upper surface of the wings is bordered with white. The white brim is accompanied by superficial orange pigment on its inner side. (4) A number of black dashes on the boundary between the orange band and the green centre and some more in the green area. (5) A black stripe on each side, in front of and behind the eye that begins at the base of the rhinophore and extends backwards to twice its pre-ocular length.

The rolled rhinophores extend beyond the head in front. Their inner border bears a basal lobe which projects towards the mouth. Rhinophores, sides and back of the foot, and underside of the wings are strewn with scattered warts. These form a crest on the ventral surface of the lobes and on the dorsal side of the foot. The pedal crest bifurcates in front.

The four parapodia are of equal size, 10 mm. long and up to 6 mm. broad, dorsally concave and ventrally convex. Their bases are narrow; the borders undulate. When the living snail autotomized one wing in the narcotic, no mark was to be seen, but it appeared as a dorsally open crescent (*w*) in the preserved specimen. The rich musculature of the parapodial lobes lies mostly near the epidermis; the inner connective tissue is loose and surrounds numerous large spaces. The foot is about 2 mm. high. The sole is 2 mm. broad, bliobed in front and pointed behind.

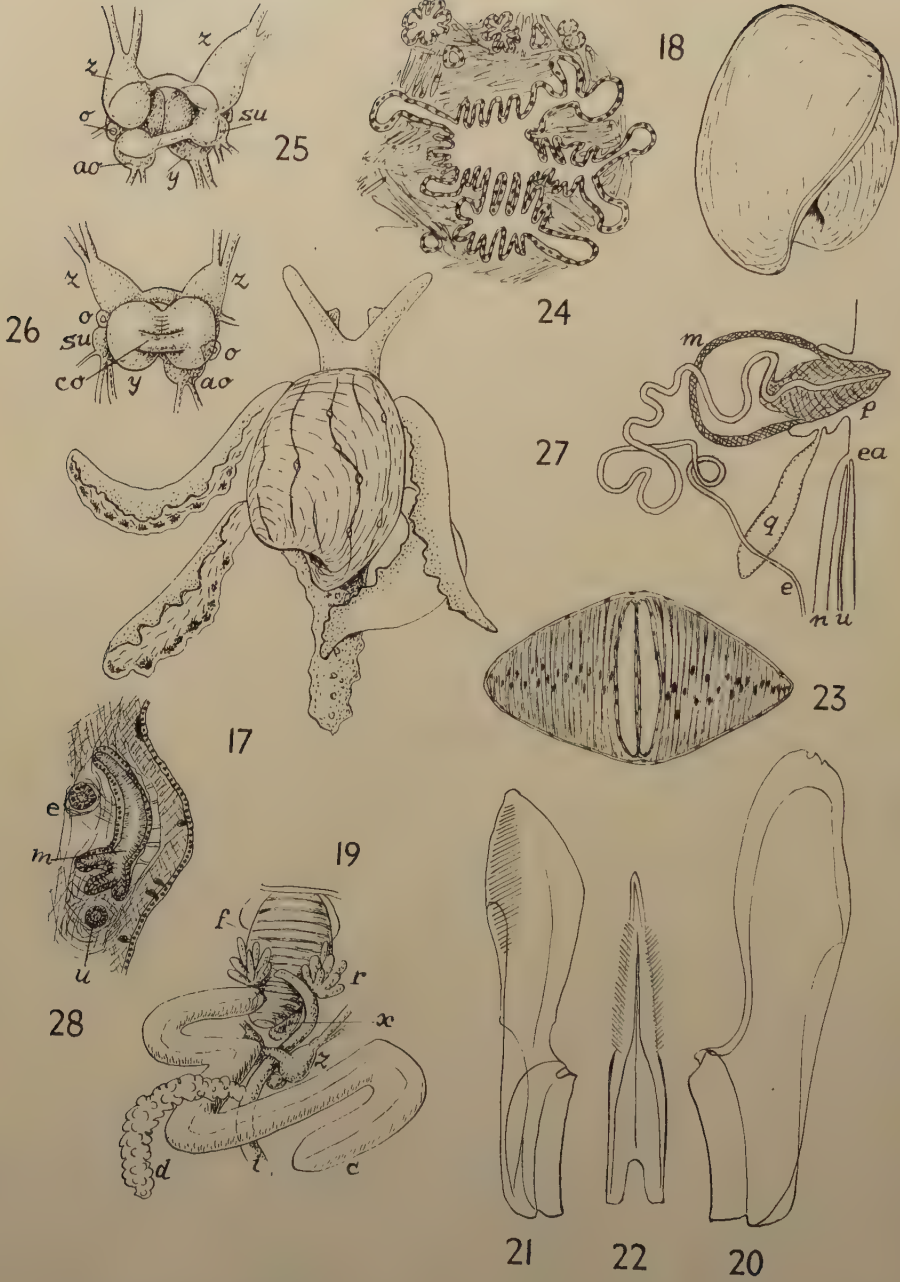
The shell (Fig. 18) is 8 mm. long, 5 mm. broad and about 3 mm. high. It is rounded in front, more pointed behind and has an umbilicated spire. The margin of the inner lip is reflexed, the outer lip regularly arcuate. The striated corneous layer is soft and colourless, the calcareous layer thin and fragile, though not completely transparent.

The mantle cavity (Fig. 29) opens on the whole length of the right side, while the dorsal and ventral mantle lobes are united in front, behind and on the left side. The anterior commissure of the mantle or pillar is narrow, but extends far to the right side. The dorsal mantle border with its shell-forming groove surrounds the whole back and bears white dots which are glands (*ia*).

The gill (*b*) is pectinate (Hoffmann, 1940, fig. 22) with about 60 longitudinal folds occupying nearly the whole breadth of the roof of the pallial cavity. The inconspicuous osphradium (*os*) in front of the gill lies on the right side. The kidney (*k*) is situated in the pallial roof dorsal to the gill and extends backwards a little beyond it. In this posterior part of the kidney the renal pore (*ni*) opens into the mantle cavity. On the right side of the gill the renopericardial duct (*re*) runs forward along the branchial border. The heart with its enormous, thin-walled auricle (*au*) shows in front of the gill, the voluminous compact hypobranchial gland (*j*) behind the gill and the free posterior part of the kidney (*k*).

The floor of the pallial cavity bulges in front because of the underlying crop (*c*). Then follows a deep furrow that stretches to the left side, and farther backwards a convexity brought about by the genital mass (*g*) continued by the digestive gland (*l*) and the ovotestis (*h*). The gut is marked along the middle of the liver and opens by a wide anus (*a*) in the floor of the pallial cavity.

The central nervous system (Figs. 25, 26) agrees with that of the European species in Mazarelli's and Pelseneer's interpretation (Hoffmann, 1936, p. 753). The cerebropleural commissure, it is true, is not as short as in *L. serradifalci*, and the visceral loop between the supra-intestinal (*su*) and abdominal (*ao*) ganglion is longer. The abdominal ganglion is only a trifle bigger than the supra-intestinal ganglion. The two cerebropleural ganglia (*z*) are of equal size. A distinct trace of the sub-



intestinal ganglion can therefore not be indicated. The fibres of the pedal commissure run internally, while those of the parapedal commissure (*co*) appear on the ventral surface.

Mazzarelli's description of the superficially lying eye of *L. serradifalci* was altered by Hoffmann (1935, pp. 626-632) with regard to the praecorneal sinus and the lens. The sinus exists in *L. souverbiei*, and the nuclei of the connective tissue cells of its anterior border project into the sinus. The ovoid lens fills the greater part of the ocular cavity. The retina consists of broad sensory cells with big spherical nuclei and slender supporting cells with ovoid nuclei. The latter probably produce the pigment.

The radula (Fig. 20) has four functional teeth in the ascending and eight in the descending limb. Their blades are compressed laterally and have a blunt notched tip. They are up to 0.4 mm. long, one-third of which belongs to the base, and are smooth. In the ascus the smaller teeth up to 0.182 mm. long are finely crenulated on both sides (Figs. 21, 22) and their point is entire, not notched. The larger teeth in the ascus measure at least 0.195 mm. and the functional ones have neither crenulation nor notched cusps.

The short oral tube is followed by the pharynx (*f*) that begins with two lateral muscular thickenings which were mentioned and drawn by Bergh (1900, p. 193, pl. 13, figs. 24, 25). The crop leaves the pharynx on its left side, but a narrower "stalk" region ("Kropfrohr" Bergh) at its origin is not developed in the present species. The crop is a sinuous muscular organ, its rhombic transverse section (Fig. 23) showing a narrow double cavity surrounded by low epithelium. These cavities continue separate to the tip of the crop where they end blindly. The short clusters of the salivary glands (*r*) open into the pharynx laterally immediately in front of the crop.

At the same level the thin oesophagus (*i*) arises in the dorsal mid-line of the pharynx. The long, tubular oesophageal diverticulum (*d*) was described as being either smooth or beset with warts (Hoffmann, 1938, p. 1078). The "warts" are actually the follicles (Bergh, 1900, p. 194) on the surface of the diverticulum (Fig. 24). This organ with its muscle layers interpenetrated by multiple epithelial folds is evidently a gland, the secretion of which is passed into the oesophagus. The gut arises from the right wall of the stomach, runs backwards and upwards to the anus (Fig. 29, *a*) opening into the floor of the pallial cavity.

FIGURES 17-28.

Lobiger souverbiei P. Fischer. (Figs 17-28.)

- FIG. 17.—Sketch of living snail.
 FIG. 18.—Shell from below.
 FIG. 19.—Anterior part of alimentary tract.
 FIG. 20.—Radular tooth more than 0.2 mm. long. Side view.
 FIG. 21.—Same from ascus, 0.17 mm. long.
 FIG. 22.—Smaller tooth from ascus, seen from the face.
 FIG. 23.—Section of crop.
 FIG. 24.—Section of oesophageal diverticulum.
 FIG. 25.—Central nervous system, dorsal view.
 FIG. 26.—Same, ventral view.
 FIG. 27.—Diagram of outer genital organs.
 FIG. 28.—Transverse section of ectal genital ducts.

a—anus. *ao*—abdominal ganglion. *au*—auricle. *b*—gill. *c*—crop. *co*—parapedal commissure. *d*—oesophageal diverticulum. *e*—vas deferens. *ea*—female aperture. *f*—pharynx. *g*—female gland mass. *h*—hermaphrodite gland. *i*—oesophagus. *ia*—glands of mantle border. *j*—hypobranchial gland. *k*—kidney. *l*—digestive gland. *m*—penial sac. *n*—oviduct. *ni*—renal pore. *o*—statocyst. *os*—osphradium. *p*—penis. *q*—accessory male gland. *r*—salivary gland. *re*—renopericardial duct. *s*—spermatocyst. *su*—supra-intestinal ganglion. *t*—spermatheca. *u*—vagina. *v*—ventricle. *w*—scar of autotomized parapodial lobe. *x*—ascus. *y*—pedal ganglion. *z*—cerebropleural ganglion.

The hermaphrodite gland (*h*) lies on the left side of the liver (*l*) from which it is not distinctly separated. In front of it and farther dorsal lies the transparent mucus gland and to the right the albumen gland. This is an opaque, yellowish organ with a meandering black line on its surface that probably marks the position of the oviduct. The brown spermatheca (*t*) lies embedded in the anterior part of the mucus gland, the spermatocyst (*s*) to the right of the albumen gland and depressed. The winding ampulla is filled with sperm and is contiguous to the underside of the female gland mass (*g*). The stomach is also situated in this region, embedded in the liver.

The male and female ducts were studied in transverse sections (Figs. 27, 28). The vas deferens (*e*) is not specially dilated and glandular. It enters a muscular penial sac (*m*) and its outermost portion runs through a muscular conical penis (*p*). The penis protrudes into the male atrium and projects from the male aperture in the specimen described. A gland with thin, folded walls (*q*) opens into the male atrium.

At the female aperture (*ea*) there open together a thin duct circular in transverse section, which is the vagina (*u*), and a wide flat tube which runs backwards between the vagina and vas deferens. The second is the nidamental duct (oviduct, *n*), subcutaneous and ciliated like the vagina. As only one animal was available, the connections between the efferent ducts and the inner organs could not be established.

Occurrence: Enseada de Guarujá, east of Santos. Near low-water line, 1 snail on *Caulerpa racemosa*; 30 November 1955.

Further distribution: Curaçao (Engel); Guadeloupe (P. Fischer); Tortugas (Thiele, 1910, p. 123).

Discussion of *Lobiger souverbiei*.

The black lines in the epithelium of the dorsal surface of the mantle were decisive for our determination. *L. nevillei* Pilsbry also has such lines, according to Smith (1889: *L. viridis* Pease, 1863). The parapodia of the Indian species, however, are so deeply incised on the borders that lobes are produced as in *L. sagamiensis* Baba (1952, p. 338; 1955, p. 40). These lobes are not developed in Engel's specimens nor in the present one. Therefore one cannot unite our species with that from Japan. Also the entire, smooth tip of the functional radular teeth of *L. sagamiensis* differs from *souverbiei*. On the other hand these teeth in *sagamiensis* are, as in our material, "in the ascending series all smooth, but those in the descending series have each a row of fine denticles on either side of the blade". Evidently our snail is older than Baba's, because we found some of the later formed, smooth plates already in the ascus.

Engel (1927, p. 113) did not mention the difference between the first teeth and the following ones. He only refers to Bergh's description of *L. philippii* Krohn, 1847 (= *serradifalci* Calcara, 1840) and said that the teeth of *souverbiei* agree with those of the Mediterranean species. Bergh's detailed description of the radula (1900, pp. 193–194) does not record any particularity of the oldest teeth, and as he examined several specimens one can be sure that this character does not occur in *L. serradifalci* (Calc.).

If the crenulation of the blade occurred regularly in the first radular teeth of the snails of the Brazilian coast, a taxonomic separation from *souverbiei* would be indicated.

Baba (loc. cit.) and Si (1931, p. 17) found their material of *Lobiger* on *Caulerpa*. The colour of the snails agrees with that of these algae, thus offering a further case of "homochromie nutritiale" (Si, 1931, p. 160).

Stiliger vanellus, sp. nov. (Figs 30–34.)

The slugs are up to 3.5 mm. long alive; the biggest preserved one is 2.2 mm. in length, has cerata up to 0.6 mm. long, and a sole 0.3 mm. broad. The living animal was colourless except for blackish-brown pigment on the back which leaves the

rhinophores and the space around the eyes free, so that a common white area on either side is brought about. Ventrally to the cerata a narrow pigmented stripe stretches along the sides of the body. The club-shaped or nearly ovoid cerata, that are especially short and thick in preserved slugs, are greenish due to the hepatic diverticula, dotted with black, and lighter at the more or less pointed tips.

The head is rounded in front, in living slugs slightly concave in the middle. The rhinophores are cylindrical. The spherical eyes are 60 micra in diameter and lie superficially beneath the epidermis, far from the cerebral ganglia. The anterior border of the foot forms two round lateral lobes separated by a median recess. In the living animals the foot is as broad as the body and ends with a rather long point. The sole is ciliated.

The cerata are directed outward leaving the dorsal middle region free. The medial cerata are bigger than the lateral ones; the distribution of the cerata is irregular. The biggest of our three slugs has 16 cerata on each side; about 7 of these 32 are full-sized, the remaining 25 are in regeneration (Fig. 34, *x*). Subepidermal glands staining pink (*g*) occur in the cerata of the present species as in many nudibranchs. The hepatic diverticula (*d*) ramify in the cerata; a blood sinus (*w*) enters the cerata from the ventral side, and a bundle of longitudinal muscle fibres (*l*) runs from the base of each cerata to its tip.

The anus (*a*) is dorsomedian and lies on a low papilla behind the level of the first cerata at the beginning of the light area. The renal pore (*r*) is located in front of the anus, a little to the left. The kidney (*k*) is a very flat sac. The heart (*h*) is small and does not appear in living slugs or whole mounts. The genital apertures are situated on the right side ventrally to the cerata; that of the male vestibule (Fig. 33, *n*) lies 0.25 mm., the oviducal opening (*y*) 0.4 mm. and that of the vagina (*v*) 0.56 mm. from the anterior end in the sectioned animal (1.32 mm. in total length).

The mouth is ventral. A few dark blue staining glands lie in front; more numerous and much more voluminous light blue ones open into the buccal cavity which extends behind the entrance to the pharynx. The labial disc is slightly cuticularized. The dark blue staining salivary glands lie dorsally around the stomach (*s*) and open with narrow, winding ducts into the pharynx. The radula consists of eight teeth, three in the ascending, five in the descending limb and several in the ascus. The teeth are up to 0.165 mm. long, and smooth, not denticulate. The tip is bluntly rounded, the bases a little less than half the length.

The oesophagus rises through the nerve ring to the ciliated stomach (*s*). Dorsal and ventral longitudinal ridges of the gastric epithelium bear stronger cilia than the rest, as in another species of *Stiliger*, the description of which is in print. The short intestine (*i*) turns dorsally. The anal papilla is curved backwards, and is 60 micra long. The hepatic diverticula (*d*) leave the stomach posteriorly to the pylorus. Two branches extend forward, supply the anterior cerata and end at the bases of the rhinophores; two branches go backwards to the posterior cerata.

The numerous globose follicles of the ovotestis (*o*) containing male and female cells surround the mucus gland (*f*). The diagram (Fig. 33) is simplified with regard to the number and position of these follicles, the hermaphrodite duct formed by the union of the ductules (*z*) which come from the follicles, and the ampulla (*m*) which extends irregularly between the folds of the mucus gland (*f*) and the stomach (*s*). The hermaphrodite duct is ventral to the mucus gland, the branched albumen glands (*b*) accompany the liver ducts, but do not go into the cerata. The spermoviduct is ciliated and divides shortly beyond its exit from the ampulla (*m*).

The vas deferens (*e*) receives a lobate, red-staining prostatic gland (*g*), runs forward, enters the muscular penial papilla (*p*) and ends with a very thin stylet (*ei*) that is directed backwards.

The oviduct (*oi*) is short. It passes into the enormous mucus gland (*f*) which receives the tubes of the albumen glands (*b*) and opens through a broad nidamental duct (*y*).

The third aperture is that of the vagina (*v*) ; it begins with a dilated outer part containing spermatozoa fixed with their heads to the wall. The long vagina runs to the spermatheca (*t*) lying far forward. It contains sperm and some secretion such as is often found in the spermatheca. The fertilizing duct (*u*) leaves the spermatheca at the entrance of the vagina and expands where it opens to the oviduct (*oi*) to form a fertilization chamber (*c*).

Occurrence : Three specimens from algae in the upper littoral were found on the coast of the State of S. Paulo at different localities, the entrance of the bay of Santos (Ilha das Palmas) ; Guarujá (east of Santos, July 1947) ; and near Ubatuba, about 150 km. north-east of Santos (September 1955).

Discussion of *Stiliger vanellus*.

The present species belongs to the true *Stiliger*. Among 22 species of *Stiliger* (and the Subgenus *Ercolania* Trinchese 1872), the descriptions of which were available, *Stiliger vanellus* comes nearest to *S. niger* Lemche (1935, p. 134) found near Nyborg, Fyn, i.e., in the Great Belt. The Baltic species is bigger, 7–8 mm. alive, its light spots around the eyes separate from those of the rhinophores, its general colour darker, and with the cerata coloured differently. Whether *S. vanellus* actually deserves specific rank is doubtful, but as the reproductive organs of *S. niger* are not known, *vanellus* cannot be united with it. However it agrees so closely with *niger* that it may have been transported by ship. Our first locality lies a few hundred metres from the place where transatlantic ships frequently wait for hours or days for their turn to enter the port of Santos. The second and especially the third localities where we found *S. vanellus* are very distant from the route of these ships. Even if the species was once brought to Brazil by ships, it has evidently established itself here.

Elysia cauze, sp. nov. (Figs 35–44.)

The biggest slug was 30 to 40 mm. long alive ; the breadth was about 6 mm. with the parapodia folded up, and 10 mm. or more when they were expanded. The foot of this living slug was 4 mm. broad, the length of the rhinophores also about 4 mm. The length of the preserved animal is 27 mm., its breadth with unfolded parapodia 15 mm., the height 0.6 mm. at the insertion of the parapodia. The general colour, a brownish and greenish-grey, resembles that of the alga *Porphyra*, did not turn into bluish-green in the fixative "Susa", but grew pale in alcohol. The foot is green. On the greenish-brown parapodia small dark rings that mark the outlets of glands occur on the outer side and white spots on the inner side, probably the female parts of the

FIGURES 29–34.

Lobiger souverbiei P. Fischer. (Fig 29.)

FIG. 29.—Mantle cavity cut open from X to X.

For lettering see Figs 17–28.

Stiliger vanellus, sp. nov. (Figs 30–34.)

FIG. 30.—Living slug, ventral view.

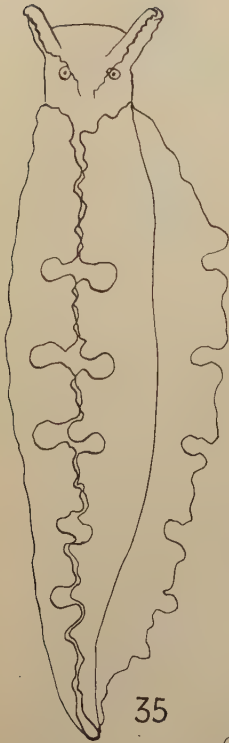
FIG. 31.—Preserved slug, dorsal view.

FIG. 32.—Tooth of radula.

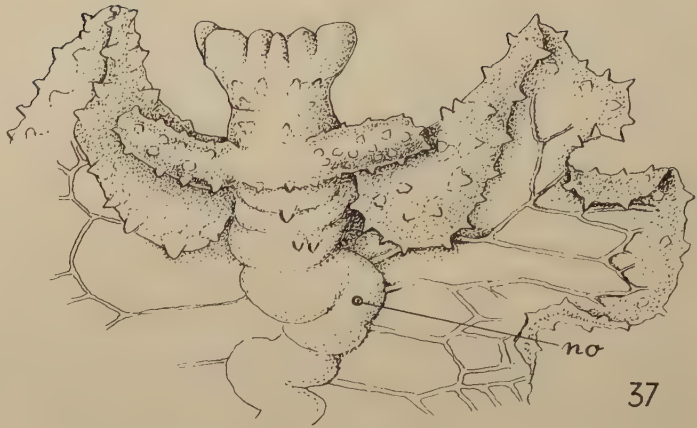
FIG. 33.—Diagram of reproductive organs.

FIG. 34.—Transverse section on level of renal pore.

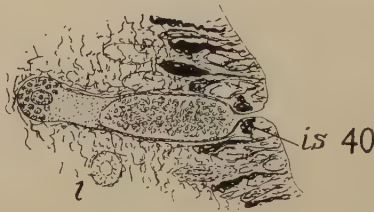
a—anus. *b*—albumen glands. *c*—fecundatory chamber. *d*—digestive gland. *e*—vas deferens. *ei*—penial stylet. *f*—female gland mass (mucus gland). *g*—glands of cerata. *h*—heart. *i*—intestine. *j*—pedal glands. *k*—kidney. *l*—muscle in the ceras. *m*—ampulla. *n*—male vestibule. *o*—hermaphrodite gland. *oi*—oviduct. *p*—penis. *q*—prostatic gland. *r*—renal pore. *s*—stomach. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—blood sinus. *x*—regenerating ceras. *y*—oviducal opening. *z*—hermaphrodite ductules.



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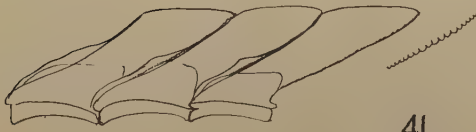
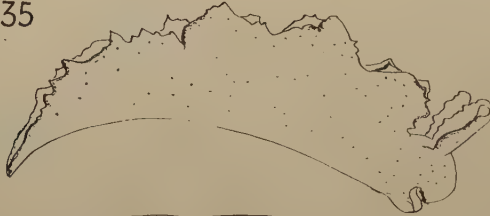


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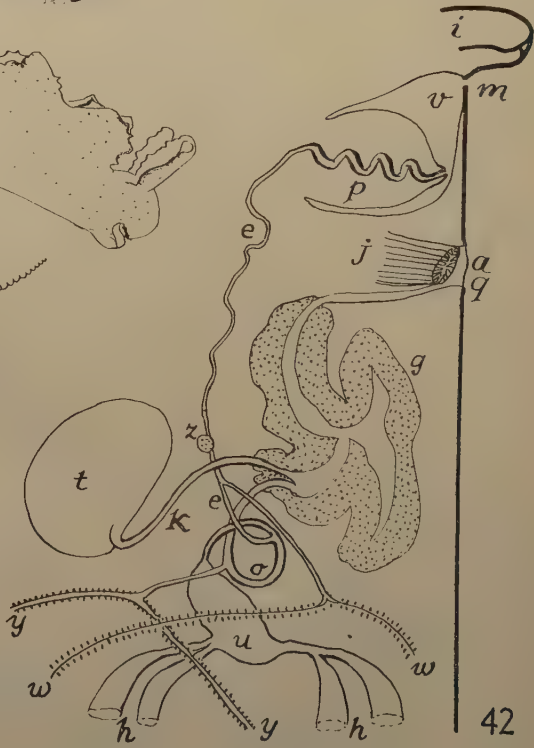
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42

hermaphroditic follicles shining through the epidermis. The big black eyes are about 0.1 mm. in diameter and lie within light areas. The labial folds and the anterior margin of the parapodia are black, the rhinophores slightly pigmented on the greenish-brown ground colour.

In the living slugs the head and neck stand out over the parapodia (Fig. 35), but with fixation the head of the largest was bent so far backwards (Fig. 37) that the anterior borders of the parapodia became the foremost elements. The aspect of the other preserved specimens is that of Fig. 39. The parapodia end on the tip of the tail. Conical and mammillate warts with white tips occur on the outer side of the parapodia, in a single row also on their inner margin, and on the rhinophores, the head, the border of the foot, and a few on the neck. The rhinophores are rolled; the margin of the parapodia is undulating, and the foot has a transverse furrow. The male pore (*m*) lies under the right rhinophore, the anus (*a*), together with the female pore (*q*), in one pit on the anterior border of the right parapodium, and the renal pore as a thick button (*no*) on the right side of the eminence over the renopericardial complex. The renal sac appears as a strong pad on the surface and continues as a long roll backwards. The epithelium of the kidney is richly folded. The body cavity is filled up with parenchymatous fibres, unlike the other Brazilian species of *Elysia*. The vessels and their anastomoses on the inner side of the parapodia are distinct.

There is a thick layer of basophil pedal glands. Some blue-staining cutaneous glands occur also on the dorsal side, where the epidermis is low except over the renal tube. Scattered giant gland cells lie on the outer side of the parapodia. They are about 0.24 mm. long and 0.04 mm. in diameter, have a long nucleus at the base, and a voluminous vacuole containing yellow granules (Fig. 40). As mentioned above, their orifices are recognizable as black rings (*is*), formed by the pigmented epidermal cells around the glandular opening. A peculiar solid and spherical organ (Fig. 44, 5*b*) of 0.6–0.7 mm. diameter lies in front of the heart in the parenchyma. It consists of a dense stroma containing cells and is not irrigated by blood vessels. Probably it is homologous to similar, possibly phagocytic organs of other Opisthobranchs, e.g. Doridids, to which the name "blood gland" has been given. We have not found any reference to lymphatic glands in the Elysiomorpha.

The central nervous system is tightly wrapped in conjunctive tissue and contains the seven components known from *E. viridis* (Russell, 1929): two dorsal cerebropleural ganglia lying close together and connected with the eyes by long tracts; two pedal ganglia ventral to the oesophagus; the visceral loop containing the left sub-intestinal, the large abdominal, and the supra-intestinal ganglion, all united by very short connectives. The biggest cell lies in the supra-intestinal ganglion and is 0.1 mm.

FIGURES 35–42.

Elysia cauze, sp. nov. (Figs 35–42.)

FIG. 35.—Dorsal aspect of living slug.

FIG. 36.—Anterior end of same from right side.

FIG. 37.—Biggest preserved slug, dorsal view of anterior part.

FIG. 38.—Head of same in ventral view.

FIG. 39.—Usual aspect of preserved slug.

FIG. 40.—Giant gland cell from side of body.

FIG. 41.—Radular teeth and edge of cusp with higher power.

FIG. 42.—Diagram of reproductive organs without ovotestis.

a—anus. *ao*—aorta. *as*—ascus. *b*—blood gland. *c*—brain. *e*—vas deferens. *f*—pharynx. *g*—mucus gland. *h*—hermaphrodite ducts. *hi*—heart. *i*—rhinophore. *is*—pigmented ring around skin gland. *j*—intestine. *k*—spermathecal canal. *l*—liver branches. *li*—diverticula of stomach. *m*—male pore. *mo*—mouth. *ni*—kidney. *no*—renal pore. *o*—oviduct. *oe*—oesophagus. *p*—penis. *q*—female opening. *r*—radula. *se*—stomach. *t*—spermatheca. *u*—ampulla of spermoviduct. *v*—male atrium. *w*—prostatic glands. *x*—oesophageal pouch. *y*—albumen glands. *z*—genital ganglion.

in diameter. The buccal ganglia are in front of the central ganglia and lie ventrally at the junction between pharynx and oesophagus.

The mouth is a vertical slit continued as a notch in the anterior border of the sole. On each side of the mouth runs a transverse fold, the labial fold, dotted with dark pigment. The voluminous pharynx (Fig. 43, *f*) (2 mm. long) has a cuticularized entrance (Fretter, 1941, p. 186), and its dorsal part is covered with annular muscles resembling the hoops of a barrel. The oesophagus (*oe*) leaves the pharynx at its hind end, not on the dorsal side as in other species of the genus. The radula (*r*) ends straight in the ascus (*as*); it contains 37 teeth, five of which belong to the dorsal limb. The oldest teeth are 25 micra long, the youngest 320 micra. The edge of the cusp bears broad, blunt teeth 2 or 3 micra broad. The salivary glands were not observed. The lateral walls of the oesophagus are folded longitudinally. The dorsal crop (*x*) is closed behind and open in front, 0.65 mm. long, 0.8 mm. in diameter, with a thick muscular wall and a 0.3 mm. wide lumen. The stomach (*se*) too, has longitudinal folds and forms two ventrolateral pouches (*li*). Each of them gives rise to two lateral hepatic ducts (*l*) and is extended into an anterior and a posterior liver duct. The intestine originates (*j*) from the middle of the dorsal wall of the stomach. It is wide, provided with high folds, and bends forward and downward, where the spacious and folded anus (*a*) opens on a level with the hind wall of the male atrium. The invagination of skin at the posterior border of the anus contains the female pore (*g*). The liver consists of richly ramified narrow tubules lined by a low epithelium.

The hermaphrodite gland is composed of a very great number of follicles in a single layer. As in other species of the genus the upper half of each follicle contains male and the lower half female germ cells. The numerous hermaphrodite ductules gradually join to form four wide ducts (Fig. 42, *h*) full of sperm near the ampulla (*u*). The latter is empty and small in the present specimen. A common spermoviduct leaves the ampulla and separates into an efferent duct (*e*) and an oviduct (*o*). Racemose eosinophilous glands open into both male and female branches, the former being the prostate (*w*), the latter (*y*) the albumen gland. The vas deferens passes near a large genital ganglion (*z*) and winds through the penial papilla, a large, unarmed cone. The mucus gland (*g*) is exceptionally small in the present specimen. Where it receives the oviduct, the latter communicates with a coiled canal (*k*), that passes to the left over the stomach and opens into a large spermatheca (*t*) containing spermatozoa and secretion.

Occurrence : Island of São Sebastião, among algae on a boulder in the upper littoral; 1 specimen, 21 November 1953. Near Ubatuba, 4 slugs on *Caulerpa racemosa*, September 1955.

Discussion of *Elysia cauze*.

Among the vast number of species of *Elysia* few are sculptured :

- (1) *E. japonica* Eliot (1913, pp. 46-47). Baba, 1937, p. 225; 1949, pp. 35, 131. Few small papillae were observed in some of Baba's slugs. As the radular teeth are smooth in Eliot's material and finely serrated in Baba's, Pruvot-Fol

FIGURES 43-48.

Elysia cauze, sp. nov. (Figs. 43-44.)

FIG. 43.—Diagram of alimentary tract.

FIG. 44.—Transverse sections 1-6 as indicated in Fig. 43.

For lettering see Figs 35-42.

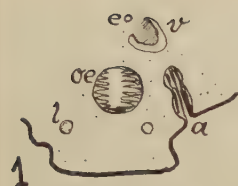
FIG. 45.—Reconstruction of alimentary tract in side view of *Elysia serca* Marc.

FIG. 46.—Same of *Elysia chitwa* Marc.

FIG. 47.—Same of *Elysia canguzua* Marc.

FIG. 48.—Same of *Elysia evelinae*, sp. nov. (See also Figs 49-57).

For lettering see Figs 49-57.

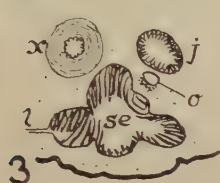


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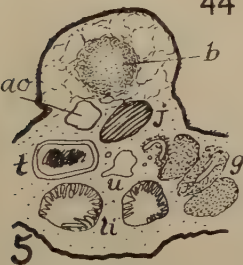


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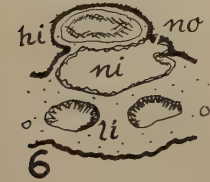


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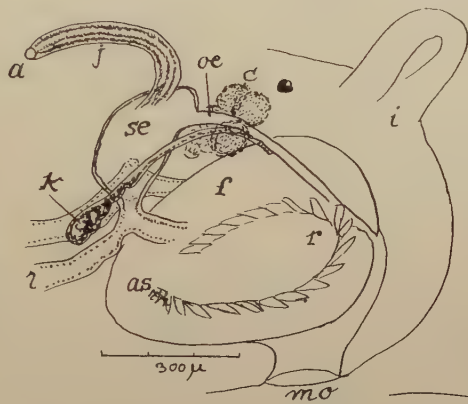
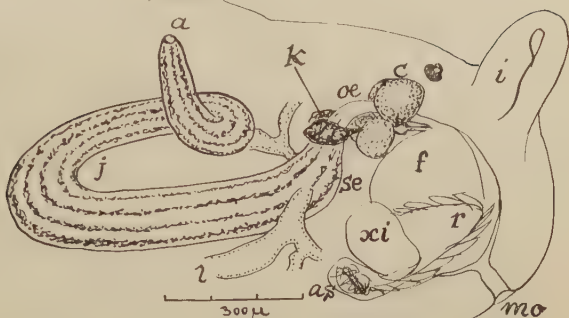
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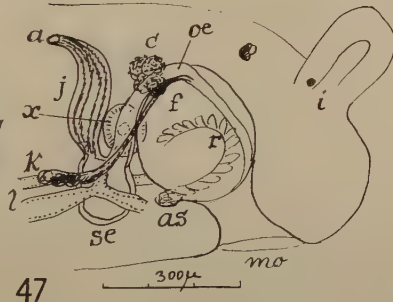
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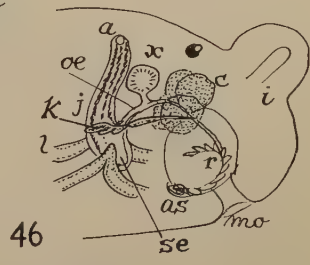
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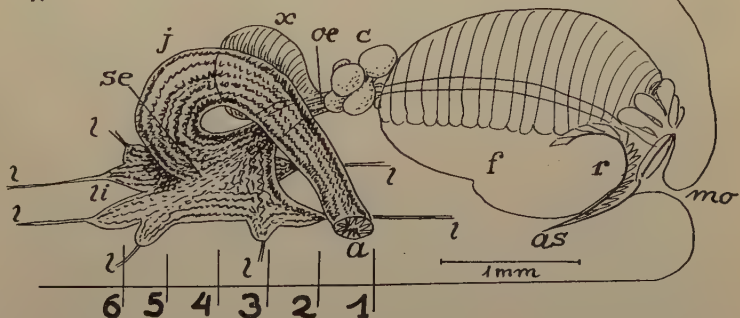
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47



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43

- (1946, pp. 37–38) questions Baba's classification. Body light chocolate or pink, covered with yellowish-white dots which are either sparsely scattered or grouped.
- (2) *E. maoria* Powell (1937, p. 121). Sparse tubercles; rhinophores without them. Dark green with black and brick-red dots. Radular tooth with smooth edge, to judge from text-fig. 1.
 - (3) *E. (Elysiobranchus) mercieri* Pruvot-Fol (1930, p. 230; 1946, p. 40). Risbec, 1953, p. 177. Four pairs of erect ramified appendages on the borders of the parapodia, the first very small.
 - (4) *E. papillosa* Verrill (1901, p. 31). Is 12 mm. long and has whole surface of body and parapodia thickly covered with papillae. Two orange-brown transverse bands on posterior side of rhinophores. The only Atlantic species with papillae.
 - (5) *E. pilosa* Risbec (1928, p. 282; 1953, p. 171). The name is not "*villosa*" (Pruvot-Fol, 1946, pp. 37, 40). Sculpture consisting of small branched white threads.
 - (6) *E. pruvotae* Risbec (1953, p. 173). Papillae on both sides of parapodia. Radular tooth smooth. Anus near male pore.
 - (7) *E. trisinuata* Baba (1949, pp. 36, 132). "Grass-green with orange dots sprinkled on the head, neck and parapodia. Small conical papillae are irregularly scattered on the outer surface of the parapodia and on the rhinophores."

***Elysia evelinae*, sp. nov. (Figs 48–57.)**

Living slugs are up to 8 mm. long, preserved ones 3–5 mm. The measurements in the following lines indicate the distance from the head in a 3.1 mm. long sectioned slug, the breadth of which is 1 mm., the height 0.8 mm. The colour is brownish-grey. A dark nuchal spot is specially developed around the anal opening; the border of the parapodia is densely pigmented. The angles of the mouth are dotted with black; some red and white points mark cutaneous glands. In the fixative "*Susa*" the brownish ground colour becomes green, as in other animals that contain yellowish and brownish chromatophores of algae, e.g. *Nygulgus evelinae* (Turbellaria, Dalyellioida). Only the black dots beside the mouth, the circum-anal spot, more or less distinct mottling on back and parapodia, and the dark streaks of the sole are preserved in alcohol.

The shape is that of a typical *Elysia* with round head, long rhinophores, narrow foot (ca. 0.4 to 0.5 mm.), somewhat prominent angles of the foot, and a ventral transverse furrow at the level of the beginning of the parapodia. These are slightly undulating and end near the tip of the pointed tail.

The anus (*a*) lies at 0.8 mm. from the anterior end, near the insertion of the right parapodium, a little to the right of the mid-line, within the dark spot. At about 0.91 to 1 mm. the kidney opens; its pore is also dorsolateral and to the right. The vaginal pore (*y*) is also located on the right side of the pericardium, at 0.9 mm. between anus and renal pore. The male pore (*m*) is situated below the right rhinophore (*i*), the opening (*q*) of the oviduct shortly in front of the anus, on the right border of the foot. The distinct pericardial eminence lies beside, neither in front of nor behind, the anus; only a few superficial vessels go out from this region. The heart is inconspicuous, the kidney a simple sac.

The pedal glands are strongly developed on the whole length of the sole. Other cutaneous glands are also numerous, staining basophil and acidophil in varying degrees. The visceral loop differs slightly from that of *E. viridis*, in that the connective between the left or subintestinal ganglion and the abdominal ganglion is so short that one bipartite left ganglion results which is larger than the supra-intestinal or right ganglion.

The mouth is a longitudinal slit. Two peculiar pigment cells lie on the sides of the oral tube. The old radular teeth are heaped up in the ascus (Fig. 48, *as*), neither coiled nor straight. The ventral limb of the radular pouch forms two lateral diverticula (Fig. 56, *vi*) with rather muscular walls and low epithelium. The radula (*r*) comprises about ten functional plates and eight in the ascus. The longest teeth measure 0.1 mm., one-third of which is the length of the base. This is as long as broad and has two prominences which fit into two pits of the following, younger tooth (Fig. 54). The length of the cusp is two-thirds of the total length, its borders are thick and terminate with a very much thickened tip. The oldest teeth in the ascus are of the common *Elysia*-type, without a strengthened tip (Fig. 55).

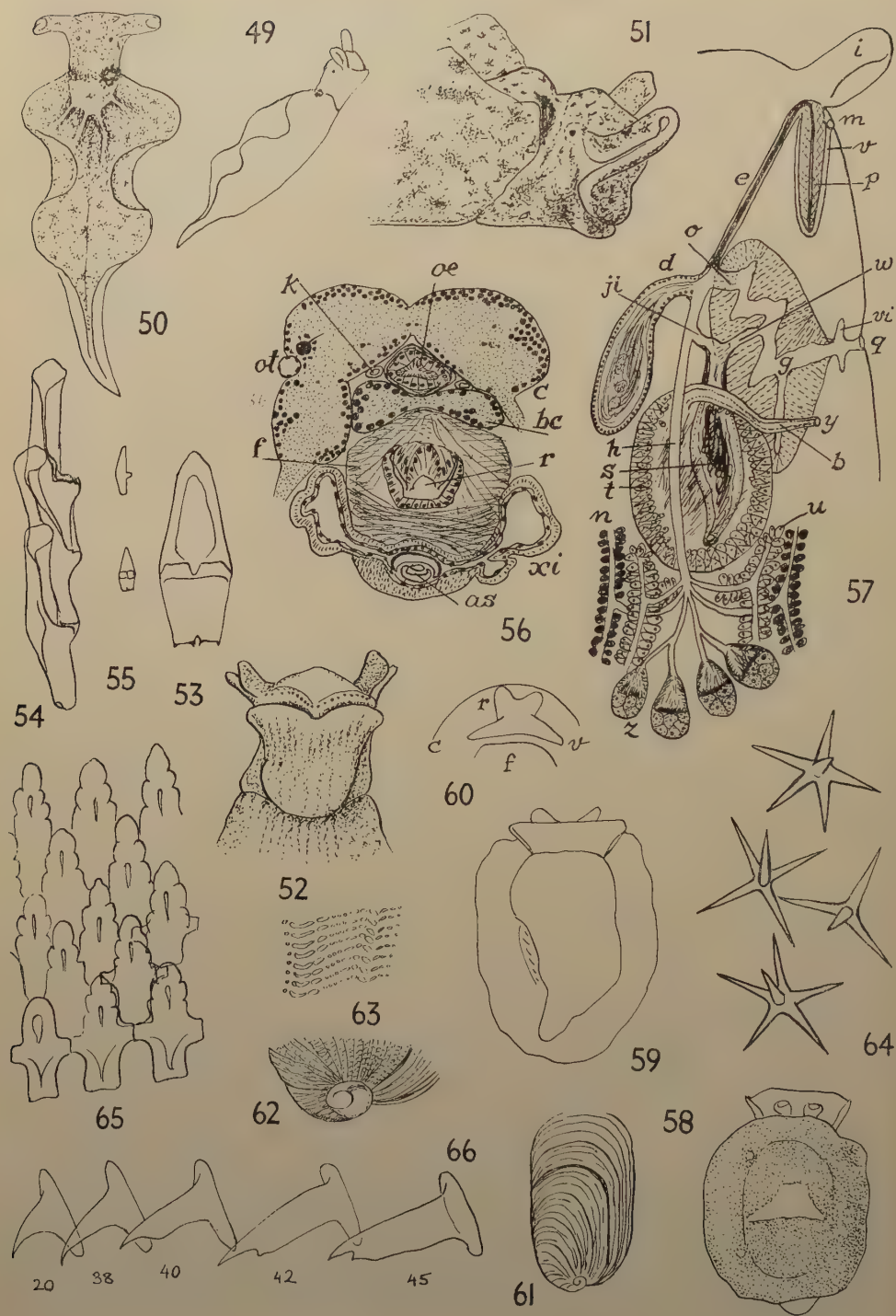
The salivary glands (*k*) are not very long, about 0.1 mm., and open, with small ampullae in the terminal part of their ducts, into the posterior angles of the pharyngeal cavity. The oesophagus (*oe*) has no dilatation and curves at 0.55 mm. to the ventral side and enlarges to an enormous stomach (*se*) with ciliated and folded lining. The gut extends posteriorly to 1.2 mm., returns forward, and the intestine opens at 0.8 mm. Stomach and intestine cannot be distinguished, both having the same longitudinal folds and narrow, high, densely ciliated cells not of secretory character. Evidently digestion takes place only in the richly ramified liver branches (*l*) that leave both sides of the stomach. The liver enters the rhinophores and lies rather superficially in the entire body. Even the most peripheral and smallest branches seem to be lined by a ciliated epithelium, visible in sections. The hepatic epithelium is infested with Sporozoa, perhaps *Coccidia*.

The numerous follicles of the ovotestis (Fig. 57, *z*) begin at about 1.2 mm. and end at 2.4 mm. There are four to six at any transverse level. They are pear-shaped, their lower half containing female, the upper half male germ cells; sometimes the two halves are separated by parenchyma. Ciliated ductules go out from the follicles and unite into at first two ducts and then a single hermaphrodite duct (*h*) runs forwards.

One branch of the hermaphrodite duct goes as oviduct (*o*) into the blue staining mucus gland (*g*) and leaves it as a short tube which forms a small chamber (*vi*) just within the pore (*q*). The male branch of the spermoviduct continues forward (*e*) and enters the penis (*p*) at 0.36 mm. The latter is 0.24 mm. long, about 0.1 mm. in diameter at its base, and lies with the point directed backwards into the male atrium (*v*), the pore (*m*) of which lies at the level of the penial base. Where the male and female branches separate, a third duct leaves the spermoviduct and turns to the left to form a vesicle which cannot be considered as an ampulla of the spermoviduct, because it is pedunculate and contains only sperm and prostatic secretion.

The vagina (*b*) passes from the vaginal pore (*y*) to the left over the mucus gland and dilates to a very voluminous spermatheca (*t*). This measures about 0.3 mm. in longitudinal and transverse direction, is 0.37 mm. high, and contains sperm in one of the sectioned slugs; it resembles the bursa of *Paludicola* or Lang's vesicle in *Polyclads* by reason of clavate, vesicular cells of its epithelium. A minute pore in the posterior ventral wall of the spermatheca communicates with a duct which dilates to a vesicle, containing sperm. This spermatocyst (*s*) opens into the mucus gland (*g*) by a fertilizing duct (*w*) and also into the hermaphrodite duct somewhat internal to the origin of the male and female branches. This canal (*ji*) between spermatocyst and hermaphrodite duct probably functions as an outlet for excess sperm.

Clusters of eosinophilous glands (*n*) lie in the posterior half of the body, near the borders of the parapodia. These are the albumen glands. Medial to them run two ciliated tubes with gland cells, the prostates (*u*). The albumen and prostatic ducts open into the hermaphrodite duct, and so the occurrence of prostate secretion in the vesicle (*d*) annexed to the spermoviduct becomes intelligible. The albuminous secretion passes into the mucus gland through the oviduct (*o*), as the direction of beating of the cilia in the canal (*ji*) between spermatocyst (*s*) and spermoviduct (*h*) inhibits a passage from the spermoviduct to the mucus gland.



Occurrence : (1) Among algae from the upper littoral of Ilhabela, island of São Sebastião, 1 specimen ; April 1954. (2) Enseada de Guarujá, island of Santo Amaro, on *Dictyota*, 6 specimens ; 18 July 1954.

Comparative notes on the alimentary and excretory organs of *Elysia* (Figs 43–48).

While the alimentary canals of four Ascoglossa, *Tridachia schrammi* (Yonge & Nicholas, 1940), *Elysia viridis*, *Limapontia capitata*, and *Hermæa dendritica* (Fretter, 1941) are very much alike, our five species of *Elysia*, *canguzua*, *chitwa*, *serca*, *cauze*, and *evelinae*, do not all agree with one another and still less with the three other Brazilian Ascoglossa, *Stiliger talis*, *Hermæa coirala*, and *Alderia uda*. *Elysia canguzua* and *E. chitwa*, as well as *Tridachia schrammi* and *E. viridis*, which all feed on green algae, e.g. *Codium*, have a muscular oesophageal pouch. Such occurs also in *E. cauze*. The fluid contents of the plant cells punctured by the radula and sucked into the buccal cavity is pumped through the stomach to the liver by this pouch (Fretter 1941, p. 194). The stomach in *E. canguzua* and *E. chitwa* is very small, the intestine short. *Elysia serca* is a greyish-brown and sometimes green species. Its food is *Sargassum* or *Padina*, and *Ulva*. Like *E. evelinae*, which feeds on *Dictyota*, *E. serca* has no oesophageal pouch, but for the rest the alimentary tract of these two brownish species differs widely. The pharynx of *E. serca* is enormous, its length one-fifth of the body length ; the stomach is small and thinwalled, the intestine very short, one-tenth of the body length, and folded. Stomach and intestine in *E. cauze* and *E. evelinae* form a morphological unit, the length of which is two-fifths of the body length in *evelinae*, much less in *cauze*. The pumping pouch of the green species and of *E. cauze* is functionally replaced in *E. evelinae* by two muscular pharyngeal diverticula (Fig. 56, *xi*) on both sides of the radular pouch.

FIGURES 49–66.

Elysia evelinae, sp. nov. (Figs 49–57.)

- FIG. 49.—Lateral view of preserved specimen.
 FIG. 50.—Dorsal view of same.
 FIG. 51.—Anterior part of other specimen in side view.
 FIG. 52.—Ventral view of same.
 FIG. 53.—Radular tooth, surface view.
 FIG. 54.—Three radular teeth in side view.
 FIG. 55.—Oldest teeth from ascus.
 FIG. 56.—Transverse section of pharynx with muscular pouches.
 FIG. 57.—Diagram of reproductive organs.

a—anus. *as*—ascus. *b*—vagina *bc*—buccal ganglion. *c*—brain (cerebropleural ganglia). *d*—vesicle of hermaphrodite duct. *e*—vas deferens. *f*—pharynx. *g*—mucus gland. *h*—hermaphrodite duct (spermoviduct). *i*—rhinophore. *j*—intestine. *ji*—canal between spermatocyst and spermoviduct. *k*—salivary gland. *l*—liver. *m*—male opening. *mo*—mouth. *n*—albumen gland. *o*—oviduct. *oe*—oesophagus. *ot*—statocyst. *p*—penis. *q*—opening of oviduct. *r*—radula. *s*—spermatocyst. *se*—stomach. *t*—spermatheca. *u*—prostate. *v*—male atrium. *vi*—pouch of oviduct. *w*—fertilizing duct. *x*—muscular pouch of oesophagus (does not occur in *E. evelinae* and *E. serca*). *xi*—muscular diverticula of pharynx. *y*—vaginal pore. *z*—ovotestis.

Berthella tupala, sp. nov. (Figs 58–66).

- FIG. 58.—Living slug, dorsal view.
 FIG. 59.—Ventral view of same.
 FIG. 60.—Velum and rhinophores. *c*—border of notum. *f*—foot. *r*—rhinophore. *v*—velum.
 FIG. 61.—Shell.
 FIG. 62.—Apical spire with higher power.
 FIG. 63.—Structure of shell.
 FIG. 64.—Spicules.
 FIG. 65.—Mandibular platelets.
 FIG. 66.—Radular teeth.

As the multiple renopericardial communications of *Elysia viridis* (Pelseneer, 1893, p. 458; 1906, p. 110, fig. 92) are unique among Molluscs (Hescheler, 1900, p. 356), we looked for these organs, which were not confirmed by Hecht (1895, p. 647) and others (Eliot, 1910, p. 178), in our five species, but did not find more than one renopericardial pore. The kidney of *Elysia canguzua* is branched in the posterior half; that of *E. serca* is anteriorly a smooth broad sac and posteriorly somewhat lobed. The kidney of *E. chitwa* is a simple sac like that of *E. evelinae*. That of *E. cauze* is very long and internally folded.

Discussion of *Elysia evelinae*.

The present species approaches *Thuridilla* Bergh (see *Elysia picta* Verr. in the following list) by its pharyngeal crop, but as its anus lies in front and to the right of the mid-line it cannot be placed in *Thuridilla*. The anatomy of most species of the Elysiidae is not known, so that it is advisable to distinguish with Pruvot-Fol (1946) only three genera, *Elysia*, *Thuridilla*, and *Tridachia*. The rules of nomenclature do not permit the adoption of Fischer's (1887, p. 545) and Thiele's (1931, p. 415) etymological correction of *Tridachia* to *Thridachia* (thridax = lettuce). The various subgenera of *Elysia* are not sufficiently characterized, perhaps with the exception of *Elysiobranchus* Pruvot-Fol (1930, p. 230; 1946, p. 40; Risbec, 1953, p. 177).

In one species of *Tridachia* a brown band around the edge of the parapodia is due to zooxanthellae in the connective tissue (Yonge & Nicholas, 1940). In the present species the chloroplasts of ingested algae suffer the colour change mentioned in connection with "Susa".

The increasing number of different species of *Elysia* found on the coast of São Paulo makes it desirable to survey the recognizable West Atlantic Elysiidae; these belong to *Elysia* and *Tridachia*.

- (1) *Elysia* (*Elysia*) *ornata* (Swainson, 1840). Verrill (1901, p. 28). Engel (1927, pp. 113-115). Parapodia edged with outer black and inner orange lines occur in this species from the West Indies and Bermudas as well as in the Indo-Pacific *E. ornata* (Pease, 1860, p. 36), but the latter has the cusp of the radular tooth more pointed and smooth (Risbec, 1928, fig. 94; 1953, fig. 121D). The Atlantic species has been redescribed by Engel (loc. cit.). Evidently Pease's species must be renamed, if it does not turn out to be identical with an older Indo-West-Pacific species (Allan, 1947, p. 439).
- (2) *E. (E.) subornata* Verrill (1901, p. 29). Border of parapodia brown (not black as in *ornata*) and orange; inner side of parapodia dark green. Rhinophores distally brown, not orange and black as in *ornata*. Surface distinctly though minutely papillose, not smooth as in *ornata*.
- (3) *E. (E.) chlorotica* Gould (1870, p. 255). Verrill (1873, pp. 480, 667). Emerald-green marked by opaque white spots with red dots scattered between them. Length 25-37 mm.; breadth, when folded, about one-fifth the length, when fully expanded, equal to three-fourths the length. From Boston Harbour to New Jersey (Miner, 1950, p. 674).
- (4) *E. (E.) catula* (Gould, 1870, p. 256). Sea-green, shading into brownish, especially anteriorly. A whitish longitudinal mark on median line between the short blunt tentacles. A round whitish spot near middle of margin on outer side of parapodia. Length about 6 mm. From Boston to New Jersey (Miner, 1950, p. 674).
- (5) *E. (E.) flava* Verrill (1901, p. 30). Pruvot-Fol (1946, p. 35). Light yellow mottled with brown. Outer side of parapodia olivaceous stippled with white; border white; inner side almost black. Rhinophores small. Bermuda.

- (6) *E. (E.) picta* Verrill (1901, p. 30). Head, back, sides of neck reddish-brown, front of head bright red. A purple spot between anterior ends of parapodia that have blue, red, and yellow borders. White cross on head. Bermuda.

As such bright colours occur in *Thuridilla* Bergh (1872a, p. 199; 1886, p. 20), Pruvot-Fol (1946, pp. 35, 41) thinks that *E. picta* possibly belongs to this genus. But as the anatomy of *E. picta* is not known, while *Elysia splendida* Grube (1861, p. 133), the type of *Thuridilla*, has its anus farther behind than *Elysia* (loc. cit., pl. 1, fig. 3; Bergh, 1872a, pl. 24, fig. 18, c) and has a pharyngeal crop, *E. picta* cannot yet be ascribed to *Thuridilla*.

- (7) *E. (E.) papillosa* Verrill (1901, p. 31). Pruvot-Fol (1946, p. 36). Bluish-grey with grey and white spots; border of parapodia white; orange bands on rhinophores; parapodia densely covered with small papillae. Bermuda.
- (8) *E. (Elysiella) verrilli* Thiele (1931, p. 415). Head and greater part of back nearly black; outer side of parapodia greyish, inner side of parapodia and folds of hind part of back whitish. Woods Hole region.

Verrill 1872 (*Am. Journ. Sci.* ser. 3, v. 3, p. 284), Bergh (1886, p. 17), and Johnson (1934, p. 153) consider this species as identical with *E. catula* (Gould), but Thiele separates it. The material mentioned as *Elysiella catulus* by Verrill (1873, pp. 480, 668) was described as bright green, and seems to be identical with Gould's species.

We agree with Pruvot-Fol (1946, p. 40) who restricts the subgenus *Elysiella* to *E. pusilla* Bergh (1872a, p. 201) with a "subcarinate" head. As *Elysiella* Verrill, 1872 is older than *Elysiella* Bergh, 1872 (Wheat, 1918), the latter should be renamed or, even better, dropped.

- (9) *E. (Elysia) canguzua* Marcus (1955, fig. 45). Green with black inner side of rhinophores. Radular teeth finely serrate. No pharyngeal crop; oesophageal muscular pouch; stomach and intestine very small (all contrary to *evelinae*). No vaginal pore; only one seminal receptacle (different from *viridis* and *evelinae*); no ampulla on efferent duct near penis (as in *evelinae*; contrary to *viridis*).
- (10) *E. (E.) serca* Marcus (1955, fig. 49). Brownish with purple area between parapodia as in *E. picta* (no. 6 of this list), but without the pattern of bright colours of *picta*; or green with white spots and stipples and a black line along the margin of the parapodia, without red points. Inner side of rhinophores black. Radula denticulate. Alimentary tract characterized by enormous pharynx, oesophagus without muscular pouch, small stomach, short intestine. No vaginal pore; only one female vesicle.
- (11) *E. (E.) chitwa* Marcus (1955, fig. 53). Colour similar to that of *canguzua* (no. 9), though inner side of rhinophores white. Radular teeth nearly smooth. Digestive organs like those of *E. viridis* and *E. canguzua* with muscular pouch of oesophagus. No vaginal pore; only one seminal receptacle with a long fertilizing duct.
- (12) *E. (Elysiopertus) pruvotfolae*, nom. nov. pro *Elysia (Elysiopertus) verrilli* Pruvot-Fol (1946, p. 39); non *Elysia (Elysiella) verrilli* Thiele, 1931 (no. 8 of this list). *Elysia crispera* Mörch from Bermuda, as Verrill described it (1900, p. 547, pl. 66, fig. 4), is a light green *Elysia* with white specks and larger blotches. Its parapodia are extended over the head but not united in front as in *Elysia (Tridachia) crispata* Mörch, 1863. Engel (1927, p. 115) mentioned this fact, and Pruvot-Fol altered the name, but that must unfortunately be changed once more, if Verrill's erroneous name "*crispa*" is not considered as sufficiently different from *crispata*. Eliot (1906a, p. 688) used *crispa* Verrill.
- (13) *Tridachia schrammi* Deshayes (1857, p. 142). Caribbean islands and coast of Venezuela. Bergh (1872a, p. 191) and Engel (1927, p. 115) use the specific name *crispata* Mörch, 1863 (p. 40), because they consider it merely probable

that Deshayes' and Mörch's species are identical. Pruvot-Fol's examination (1946, p. 42) of Deshayes' specimens preserved in the Museum of Paris however validates the older name, which, it is true, was first written in this form by Mörch.

- (14) *Tridachia whiteae*, nom. nov. Described as *Tridachia ornata* (Pease) from Dry Tortugas, Florida, by White (1952, p. 118). *Pterogasteron ornatum* Pease, 1860 (p. 36) was called *Tridachia ornata* (Pease) by Bergh (1872a, p. 191), but he placed it in *Elysia* later on (1881a, p. 79, pl. G, fig. 18; 1905, p. 84), where it still has its place (Risbec, 1928, p. 280; 1953, p. 168). The parapodia separated in front (character of *Elysia*), their black edge, the smooth border of the radula tooth, and the absence of a vaginal pore (Risbec, 1953, fig. 121A) distinguish Pease's Indo-Pacific *Elysia* from White's West-Atlantic *Tridachia*. The colour of *Tridachia schrammi* Desh. differs from that of White's species, the radular teeth do not agree completely, and Bergh (1872a, pp. 191-198) described only one female pore in *schrammi*.

Berthella tupala, sp. nov. (Figs 58-69.)

The larger living slug was 12 mm. long, about 7 mm. broad and 2 mm. high. The length of the preserved animal was 7 mm. The broad mantle covers nearly the whole body of the creeping slug (Fig. 58), only the rhinophores and the velum projecting, and sometimes also the tip of the foot.

The light ochre notum is delicate with a rough surface. It has a white trapezoid mark in the middle and four to six white spots. The dorsal side of the foot is light yellow, the sole white.

The strongly calcified brown shell (Fig. 61) is 5 mm. long, 2.8 mm. broad and 1 mm. high. The rings of growth are distinct, and longitudinal sculpture lines run transversely to them. The apical spire (Fig. 62) is hardly prominent. In the preserved slug the shell covers all inner organs, the eyes, for example, lying far behind its anterior border; in the creeping slug just in front of the shell. The connective tissue

FIGURES 67-78.

Berthella tupala, sp. nov. (Figs 67-69.)

FIG. 67.—Ventral view of head.

FIG. 68.—Jaw plates.

FIG. 69.—Diagram of reproductive organs.

a—ampulla. *b*—gill. *d*—oviducal aperture. *e*—vas deferens. *g*—female gland mass. *h*—hermaphrodite duct. *j*—genital papilla. *m*—mouth. *n*—male atrium. *o*—oviduct. *p*—penis. *q*—accessory prostate. *s*—spermatheca. *t*—border of shell. *u*—fertilizing duct. *w*—vagina.

Glossodoris neona Marc. (Figs 70-72.)

FIG. 70.—Male organs.

FIG. 71.—Female organs.

FIG. 72.—Section of sheathed part (*k*) of vas deferens.

a—ampulla. *e*—outer vas deferens. *g*—female gland mass. *h*—hermaphrodite duct. *j*—spermoviduct. *k*—sheathed part of efferent duct. *m*—muscular part of vas deferens. *n*—oviducal opening. *o*—oviduct. *p*—penial papilla. *q*—thinner prostatic part. *r*—thicker prostatic part. *s*—spermatoecyst. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—fertilization chamber.

Hallaxa aepfae, sp. nov. (Figs 73-78.)

FIG. 73.—Living slug in dorsal view.

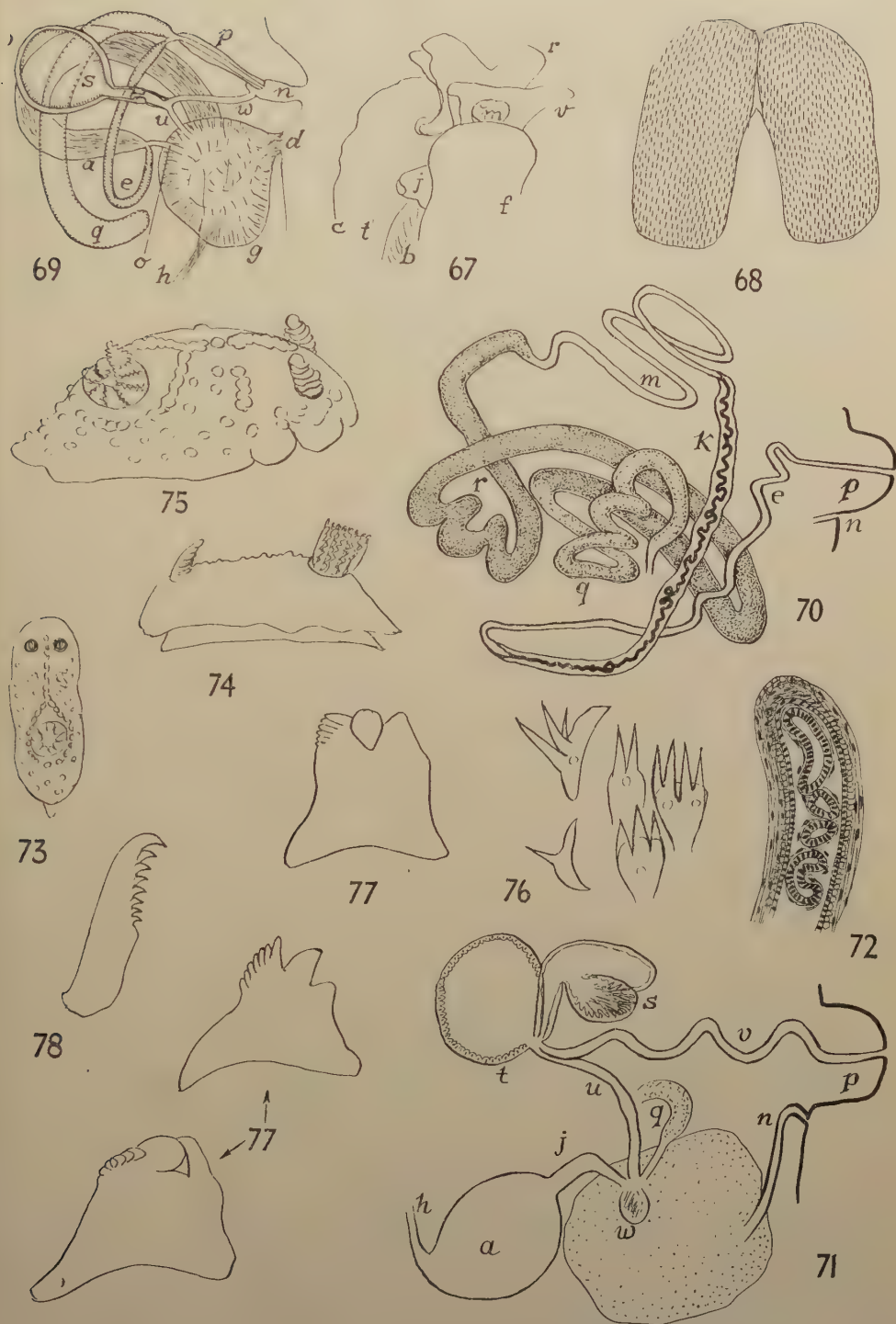
FIG. 74.—Same from left side.

FIG. 75.—Right side view of preserved slug.

FIG. 76.—Elements of labial plate.

FIG. 77.—Three innermost teeth of radula.

FIG. 78.—Lateral tooth of same.



of the very soft notum contains stellate spicules (Fig. 64), about 0.1 mm. in diameter. Their four to eight thin rays are directed to all sides and thus lie in different planes.

The anterior border of the foot (Fig. 60, *f*) is entire, neither furrowed nor notched. The sole is narrow, about 3 mm. broad. The tail is rather long and as in the other species of *Berthella* and *Berthellina* without a concentrated pedal gland. The velum (*v*) is broad and straight in front. Its outer sides as well as those of the rhinophores are furrowed and their margins rolled up. In the living slug the dorsal margin of the rhinophore bears a knob. The sensory pad on the base of the rhinophores, observed in *B. agassizii* MacFarl. (Marcus, 1955, fig. 72), occurs also in *B. tupala*. The rhinophores (*r*) are white; their common base lies between velum and notum (Fig. 67, *c*).

The gill (*b*) is small; it measures about one-fourth of the body length and has about twelve pinnules on each side of the smooth rhachis. The anus lies at the end of the branchial membrane which is inserted between second and last third of the gill. The orifice of Bourne's gland is located above the genital papilla (*j*).

The pharyngeal bulb is broad and flat. The thin and colourless mandibles (Fig. 68) are united in front, 0.525 mm. long, 0.25 mm. broad, and diverge backwards. The platelets (Fig. 65) stand in alternating series in 44 longitudinal and 32 transverse rows. The borders are denticulated in a peculiar manner, the tip of the cusp as well as the two denticles of each side being rounded. The pale radula is 0.63 mm. long and 0.5 mm. broad. It consists of 55 rows and each half-row of 50 teeth. The innermost tooth is smallest (base 10 micra, apex 8 micra), towards the middle of the row the size increases (20th tooth: base 25 micra, apex 17 micra) and still farther outwards (straight cusp 20 micra). The six to eight outermost teeth have a more or less distinct second cusp (Fig. 66).

The hermaphrodite gland is associated with the liver, but is in a reduced state in the present specimen. Notwithstanding the tubular winding dilatation of the hermaphrodite duct (*h*), the ampulla (*a*), is still full of sperm. At the anterior end of the ampulla male and female ducts separate. The first, the narrow vas deferens (*e*), has prostatic epithelium lining the whole of its long, forward running course. It receives the accessory prostate (*q*) shortly before it enters the penis (*p*). This prostate is a long muscular tube which extends far backwards and is lined with a glandular epithelium containing pink granules. The muscular male organ has a narrow lumen. It projects into the male atrium (*n*) on a small papilla and is acrembolic. In the living slug the male vestibulum was extroverted and formed a projecting papilla (*j*).

A narrow but long vagina (*w*) leaves the male vestibulum, gives off the fertilizing duct (*u*) to the female gland mass (*g*), and passes through a broad sphincter to the spermatheca (*s*). The spermatozoa stick in the epithelium of the latter with their heads. The oviduct (*o*) is short. The oviducal aperture (*d*) is wide, folded and partly ciliated.

The very spacious kidney lies dorsal to the liver in front and is ventral behind. It is stuffed with yellow crystals resembling Hecht's description and figure (1895, p. 648, pl. 4, fig. 49) of *Calma glaucooides* Ald. & Hanc. Hecht's slugs had been collected in summer, ours in winter. The renopericardial duct lies far in front.

Occurrence: 14 km. west of Ubatuba, 1 slug among algae in the upper littoral; July 1955. Ilhabela, 1 specimen under stone in the upper littoral; November 1955.

Discussion of *Berthella tupala*.

The species belongs to the genus *Berthella* Blainville, 1825, formerly *Bouvieria* Vayssière, 1896 (see Odhner, 1926, pp. 19-22; 1939, pp. 15-20). It comes into the group of species with large shell and with anus at the posterior end of the branchial membrane. Of this group two species are already known from the Atlantic coast of South America, *B. patagonica* (d'Orbigny, 1837, p. 204; Bergh, 1898, p. 496) and *B. agassizii* (MacFarland, 1909, p. 59). *B. patagonica* differs from *tupala* by its foot

which overhangs the mantle on all sides; the mandibular platelets bear three to five pointed denticles on each side; and the outermost teeth on the radula are, together with the innermost, smaller than those in between.

B. agassizii known from the coast of São Paulo (Marcus, 1955) has no spicules, contrary to *aurantiaca* and *tupala*. From both species *agassizii* differs also in that the outermost radular teeth decrease gradually in size. The platelets of the jaws have 3 to 6 pointed lateral denticles.

Further species of *Berthella* which must be compared with *tupala* are *stellata* (Risso) and *aurantiaca* (Risso). For *B. stellata* Vayssière's descriptions (1898, p. 302; 1913, p. 222; 1931, *Bouvieria stellata*) are decisive, not that of Pilsbry (1896, p. 194). Accordingly *stellata* differs from *tupala* by a cross-shaped light spot in the middle of the back surrounded by many smaller dots; by a strongly convex shell, the prominent apex of which is curved to the left side; by four pointed lateral denticles on the mandibular platelets; and different measurements of the radular teeth. These are 80 in a half-row, and about the 60th is highest.

Reliable descriptions of *B. aurantiaca* are those of Bergh's material from the Azores (1892, p. 26) and Vayssière's (1885, p. 115; 1898, p. 209; 1913, p. 220; 1932, *Bouvieria aurantiaca*). Bergh's specimen from Norway (1898a, p. 120) belongs to another species (Odhner, 1939, pp. 20, 22). *B. aurantiaca* has the outermost teeth of the radula as slender as *tupala*, but bifid ones have not been described. Neither do the rounded denticles of the mandibular platelets occur in *aurantiaca*, though the denticles vary in the different parts of the jaws (Bergh, 1892, p. 27, pl. 4, figs 26, 27; Risbec, 1931, p. 86, figs 59-61). The length of the jaws of *aurantiaca* is less than twice the breadth, while in *tupala* it is more than twice the breadth. All the rays of the spicules of *aurantiaca* lie in one plane, contrary to *tupala*. The mantle of *aurantiaca* covers the body only partially so that the foot generally projects on all sides.

Reproductive organs of *Glossodoris neona* Marcus. (Figs 70-72.)

More material of this species collected under stones in the upper littoral of S. Paulo, near Ubatuba, allowed us to examine the reproductive organs with a view to a possible future grouping of the numerous species of *Glossodoris*.

The ovotestis consists of several lobes that lie embedded in the dorsal surface of the liver over the entire length of this organ. The two animals sectioned had ripe sperm and many young gonocytes but not yet any oocytes. The muscular hermaphrodite duct (*h*) enters the hind end of the 0.4-mm. long ampulla (*a*). The spermoviduct (*j*) leaves it nearly at its anterior end.

The male duct begins as a prostate with an epithelium containing red-staining granules. The prostatic part is at first narrow (*q*) and then becomes wider (*r*). It is very long and twisted. The following muscular portion (*m*) of the efferent duct is thinner and also winding. The male duct of *G. amoena* (Cheeseman) has an inner narrow and an outer wider part (Odhner, 1934, fig. 15), which is quite uncommon in *Glossodoris*. Looking through some diagnoses of Bergh and others, e.g. White (1952) and Risbec (1953), we found an inner thick prostatic and an outer thinner part of the male duct in *G. crossei* (Angas), *edenticulata* White, *eliasbethina* (Bergh), *hilaris* (Bergh), *lineolata* (van Hasselt), *mariana* (Bergh), *mariei* (Crosse), *marginata* (Pease), *porcata* (Bergh), *sannio* (Bergh), *punctilucens* (Bergh) (Odhner, 1932, fig. 5) and *sycilla* (Bergh).

The winding muscular part of the vas deferens (*m*) is followed by a straighter one (*k*) in the present species. Here a muscular sheath (Fig. 72) encloses the twisted duct. Such a muscular sheath of the efferent duct occurs also in *G. eliasbethina* (Bergh, 1877a, p. 466) and *G. rudolphi* (Bergh, 1880a, p. 19). The outer part of the male duct, the muscular ejaculatory duct (*e*), is as long as the sheathed part, but thinner and has no sheath. Its course is somewhat sinuous, and it opens on a papilla

(*p*) produced by partial evagination of the genital vestibulum. In the second sectioned slug there is no penial papilla.

In the specimen with the so-called penis the opening of the vagina (*v*) is also located on the papilla, 50 micra behind the male aperture. The folded oviducal opening (*n*) lies still farther behind, no longer on the papilla but in the posterior wall of the genital atrium.

The female duct (*o*) which arises from the spermoviduct (*j*) opens into the female gland-mass (*g*) rudimentary in the sectioned animals. The long and sinuous vagina (*v*) enters the spherical spermatheca (*t*) by a short broad duct. The epithelium of the spermatheca is formed of cells which are united at their base, but separated at the apex where the nuclei lie. In the two present specimens spermatheca and spermatocyst (*s*) are empty. The latter is united with the vagina by a wide muscular duct. The ectal part of the spermatocyst has relatively low epithelial cells, while those of the inner part, separated by a fold, are club-shaped and ciliated. The fertilizing duct (*u*) comes off from the same point as the seminal receptacles. A dilatation of the fertilizing duct, the fertilization chamber (*w*), lies at the ental end of the duct in the gland-mass. This chamber, in both the animals sectioned, contains sperm, which seem to be derived from the animal's own gonad rather than from mating.

A vestibular gland was not found.

Doris verrucosa Cuvier. (Fig. 90.)

Our single slug of November 1953 and the great number of strongly contracted animals in the former "Museu Paulista" did not allow an exact description of the anterior border of the foot. As the details of this part are of some weight in the systematics of Doridids, we now describe it based on many living slugs and some preserved after anaesthetization. The longitudinal fold extended to the anterior part of the sole of our original figure (Marcus, 1955, pl. 12, fig. 107) is indeed produced by contraction. The anterior border of the foot is normally entire, not notched in the middle and transversely grooved. In a gliding slug this border is simply curved; when the animal stops and contracts, the border becomes irregularly folded and so it also appears in preserved specimens (Fig. 90).

The biggest slug was 55 mm. alive, and has sixteen gills. Preserved it is 35 mm. long, 20 mm. broad and 12 mm. high. The notal brim is 3 mm. broad, the foot 27 mm. in length, 14 mm. in breadth and has folded borders.

For readers who do not know the synonymy of *Doris verrucosa* Cuv. (Pruvot-Fol, 1954, p. 232) we mention that it is the species that in Lange's catalogue (1949, p. 116) figures as *Doridigitata derelecta* P. Fischer, 1867 from the coast of Santa Catharina. It was also described from Rio de Janeiro as *Staurodoris januarii* Bergh (1878, p. 583). The identity of the latter with *D. verrucosa* was established by Ihering (1886, p. 230; 1915, p. 142) and accepted by Bergh (1904, pp. 38-39).

Our new material was observed laying eggs in November. The egg ribbons are coloured yellow by the eggs and are counter-clockwise spirals forming two to three whorls 8 to 15 mm. broad. The upper margin of the ribbon is longer than its base and therefore wavy. Both ends of the ribbon are truncate. One preserved ribbon was 4 cm. in diameter, its base about 25 cm. long. The diameter of the eggs is about 80 micra. The 500,000 - 1,000,000 eggs of one ribbon are in about the same stage of development. The oblong egg capsules contain three to six eggs, but occasionally only one or two. The capsules are closely arranged in transverse wavy rows. The egg masses were fixed to the surface of stones above the low-water line, and were partly exposed at low water.

Occurrence: Island of São Sebastião, in low water near Ilhabela; 14 and 15 November 1955.

Hallaxa afeae sp. nov. (Figs 73-80.)

The living animal was 7 mm. long, 6 mm. broad and rather flat. The body is rounded in front, has parallel sides and a pointed foot, the hind end of which may protrude beyond the notum that covers the whole body. The colour is yellowish-grey with a darker liver shining through the notum and black chromatophores in the connective tissue. The gills and also the leaves of the rhinophores are pigmented.

There are scattered low bosses on the notum, several of which sometimes form a short continuous row. A longitudinal series of bosses lies in the mid-line between rhinophores and gills. In front of the branchial pouch this series bifurcates and its branches surround the pocket.

The free edge of the notum is thin and 2 mm. broad; its lobulate shape on the right side is evidently due to previous injuries. The foot (*f*) is 4 mm. long in the preserved, 6 mm. long, slug and 1.5 mm. broad in the middle, broader in front and pointed behind. The anterior border of the foot is bilabiate, not notched in the middle. Its corners are united with the oral disc by cutaneous folds that bear a wing-shaped dilatation (Fig. 79, *x*). There are no free labial tentacles dorsal to these folds as occur in *Trippa ornata* Bergh (1877*b*, p. 544, pl. 58, fig. 3, *a*), but perhaps the wings may be interpreted as tentacles as in *Phlegmodoris* (= *Trippa*) *mephitica* Bergh (1878, p. 594).

The rims of the rhinophorial and branchial pockets are smooth. The rhinophores have seven or eight leaves of different size. There are nine unipinnate gills.

The oral tube is folded longitudinally. The cuticle of the labial disc is composed of tooth-like platelets ending in two to four or more cusps. The radula has the formula 30×9 to 11, 1, 0, 1, 9 to 11. The first lateral tooth has a broad, bilobate base and its apex is divided into an inner and an outer lobe. The inner is broad, blunt and smooth, the outer bears a series of about eight cusps. Of these the innermost is biggest; those following outwards decrease in size. The rest of the lateral teeth are all alike; they have a narrow base and a flattened, slightly curved blade with about eight denticles on its margin.

The oesophagus runs backwards along the inner side of the ampulla and opens into the stomach. The lumen of the latter is not set off from the liver. The intestine leaves the stomato-hepatic cavity behind and dorsally; it begins with longitudinal folds and runs forward; later on it is smooth and narrow. Then it curves to the right side and continues straight backwards. Beside the pylorus a slender caecum protrudes from the liver curving from the left to the right side, where it nearly attains the body wall. The stomato-hepatic cavity contains animal cells without spicules. The branchial glands are very voluminous.

When the animal was dissected, light-coloured strands escaped; these belong to the hermaphrodite gland that lies around the liver. The present slug is in the male phase with only few young oogonia. The ciliated hermaphrodite duct (*h*) is rather strong. It opens into a nearly spherical ampulla (*a*) full of sperm. The short spermoviduct (*o*) enters the female gland mass (*g*). Multiple oviducal openings lead the eggs to the common genital vestibulum (*w*).

The efferent duct (vas deferens) comes out of the gland mass with a wide, glandular, prostatic part (*q*) not distinctly set off from the gland mass. The following muscular part (*e*) of the efferent duct is shorter than it is drawn in the diagram. The outermost part is surrounded by a muscular sheath (*p*) and forms an acrembolic penis. The heads of the spermatozoa are relatively long as in *H. indecora* (Vayssière, 1912, p. 36, pl. 5, fig. 66).

The long vagina (*v*) begins with a small papilla in the genital vestibulum (*w*) near the male opening. The spermatheca (*t*) and the spermatocyst (*s*) are arranged after the vaginal type (Odhner, 1926, p. 51). Besides these two seminal receptacles there is a further vaginal diverticulum (*d*) distal to the fertilizing or uterine duct (*u*).

A vaginal cone that projects into the spermatheca (*t*) constitutes an uncommon feature.

Occurrence: Ubatuba, under a stone near the high-water line, one slug in November 1954.

The species is named for Mme. Alice Pruvot-Fol with her monogram.

Discussion of *Hallaxa apefae*.

The two previous species of the genus, *H. decorata* (Bergh, 1878, p. 572) and *H. indecora* (Bergh, 1905, p. 115) are Indo-West-Pacific. The range of *Hallaxa* extends from Japan (Baba, 1949, p. 149) to the Red Sea (O'Donoghue, 1929, p. 814). As Baba (p. 61) indicated, Vayssière's (1912, p. 38) and O'Donoghue's material from the Gulf of Aden and the Gulf of Suez respectively belong to *indecora*; there is no lapsus calami (O'Donoghue, p. 721) in Vayssière's denomination of his material.

"Dorsum smooth" must be deleted from the diagnosis of the genus if it is to include the present species. Besides the notal sculpture the shape of the innermost lateral tooth also distinguishes *H. apefae* from previously described species. *H. decorata* has a finely denticulate outer lobe and a smooth, a little broader inner one, the base of which frequently has one strong, curved tooth. The corresponding tooth of *H. indecora* has a smooth outer lobe and the apex of the inner bears 2 stout, curved hooks. Multiple terminations of the teeth composing the labial armature are known of *indecora*, not of *decorata*.

Platydoris angustipes (Mörch). (Figs 81-89.)

Our only specimen is round and flat, 50 mm. long, 40 mm. broad, and about 8 mm. high. Its back was red in life; preserved it is greyish-yellow overlaid with a dark network. This is rubbed off here and there, as Allan (1932, p. 89) observed in *P.*

FIGURES 79-89.

Hallaxa apefae, sp. nov. (Figs 79-80.)

FIG. 79.—Head of preserved slug.

FIG. 80.—Diagram of reproductive organs.

a—ampulla. *d*—vaginal diverticulum. *e*—vas deferens. *f*—foot. *g*—female gland mass. *h*—hermaphrodite duct. *m*—mouth. *o*—spermoviduct. *p*—muscle sheath of penis. *q*—prostatic part of vas deferens. *r*—genital papilla. *s*—spermatocyst. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—genital vestibule. *x*—connection between foot and head.

Platydoris angustipes (Mörch). (Figs 81-89.)

FIG. 81.—Dorsal aspect of preserved slug.

FIG. 82.—Ventral view of same.

FIG. 83.—Digestive tract.

FIG. 84.—Radular teeth in different aspects.

FIG. 85.—Brain.

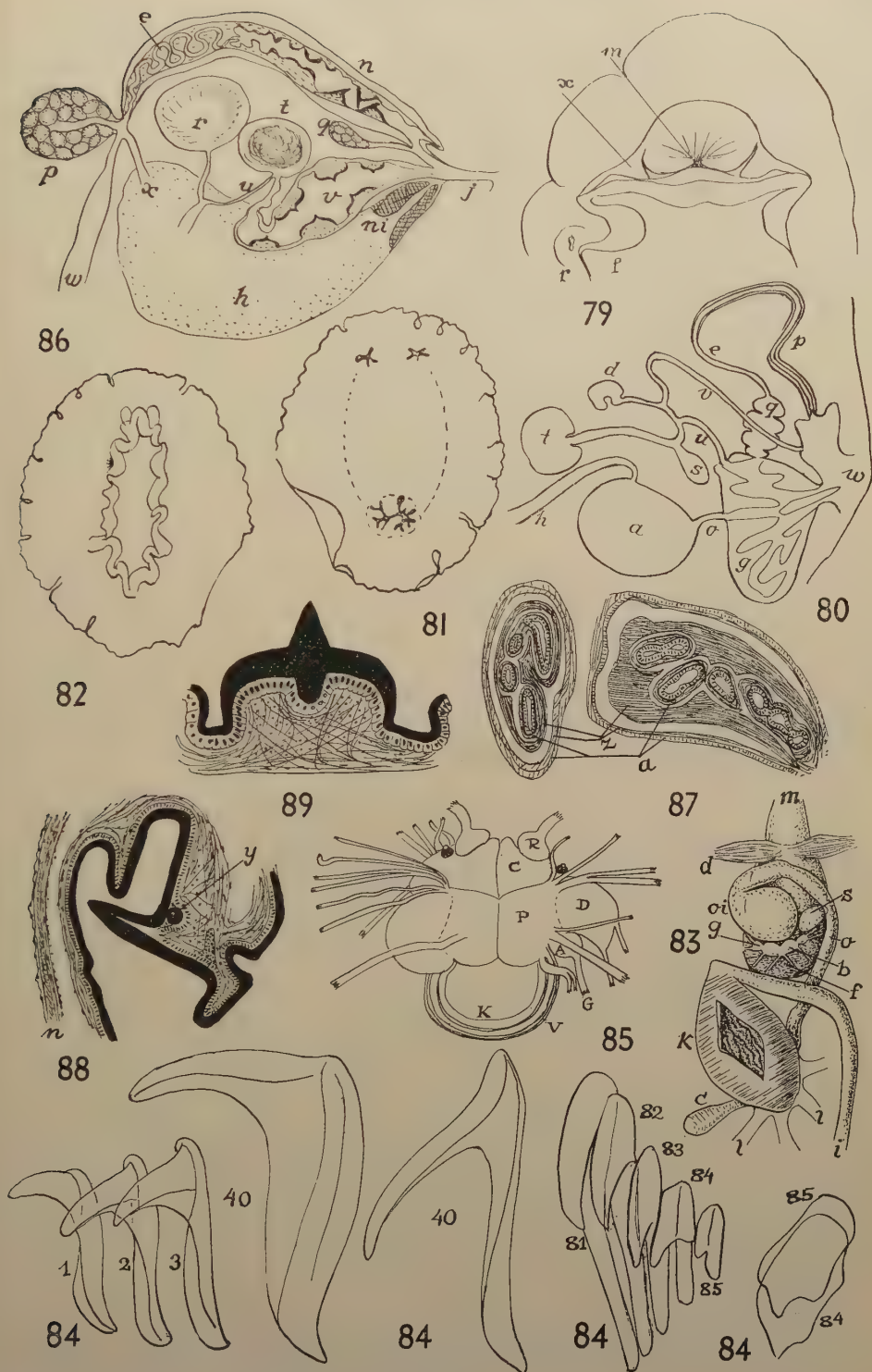
FIG. 86.—Diagram of reproductive organs.

FIG. 87.—Section of efferent duct.

FIG. 88.—Section of penial spine.

FIG. 89.—Section of vaginal spine.

a—circular muscle layer. *b*—buccal ganglion. *c*—caecum. *d*—divaricators. *e*—vas deferens. *f*—pharynx. *g*—gastro-oesophageal ganglion. *h*—female gland mass. *i*—intestine. *j*—common atrium. *k*—tritulating stomach. *l*—liver ducts. *m*—oral tube. *n*—muscular sheath of ejaculatory duct. *ni*—muscles of nidamental duct. *o*—oesophagus. *oi*—oesophageal dilatation. *p*—prostate. *q*—penial gland. *r*—spermatocyst. *s*—right salivary gland. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—ampulla. *x*—opening of oviduct into female gland mass. *y*—substituting spine. *z*—longitudinal muscle layer. *A*—abdominal ganglion. *C*—cerebral ganglion. *D*—pedal ganglion. *G*—genital nerve. *K*—pedal and parapedal commissure. *P*—pleural ganglion. *R*—rhinophoral ganglion. *V*—visceral loop.



iredalei, and leaves the minute papillae free so that these show as light dots. The underside is plain greyish-yellow and smooth. The small dorsal dots that hardly deserve the name of papillae are 70–100 micra in diameter and uniformly and densely distributed all over the notum. The latter is leathery in texture; its borders are slightly frilled and about 15 mm. broad on the sides. In front and to a lesser extent behind they are broad too.

The foot is long (30 mm.) and narrow (9 mm.); its edges are about 2 mm. broad and so much curled and contracted that only the bilabiate anterior margin could be made out. The tentacles are short and conical with lateral grooves. The distance between the pockets of the rhinophores is about 6 mm., each is 2 mm. broad, its opening 4- or 5-lobed. The rhinophores are located 8 mm. behind the anterior tip, have a smooth rhachis and 28 leaves full of parallel spicules. They are pigmented as are the six tripinnate gills. The branchial cup is 6 mm. broad and has a 6-rayed outline. It is situated 14 mm. in front of the hind end.

The spicules are abundant in all parts of the body. They are pointed or blunt, smooth or rough rods and frequently angulated near the middle. The longest complete ones are 0.7 mm. long and 40 micra thick, but there certainly occur still longer ones. The spicules of the slightly prominent notal papillae are perpendicular bundles; between them the spicules are obliquely distributed, and beneath the bundles they are parallel to the surface. Thus the disposition differs from that of Risbec's species (1928, p. 76, 81) reproduced by Hoffmann (1935, p. 551, figs 410A, B). The peritoneum is not pigmented.

The nervous system corresponds to the known scheme of the Doridacea with paired cerebropleural and pedal ganglia. As Hoffmann (1936, p. 801) had already presumed, a separation of the pleural (*P*) from the cerebral (*C*) ganglia and their coalescence with the pedal centres (*D*), described for *P. cruenta* (Q. & G.) (Risbec, 1928, p. 77, figs 9, 3), could not be confirmed. A separate abdominal ganglion (*A*) lies at the right origin of the visceral loop (*V*). The latter is united with the pedal commissures (*K*) by a common sheath of connective tissue. The buccal ganglia (*b*) lie on the hind part of the pharynx (*f*) ventrally to the oesophagus (*o*) and are each continued into a gastro-oesophageal ganglion (*g*).

The oral tube (*m*) is 5.5 mm. long and provided with enormous divaricator muscles (*d*). The cuticle of the labial disc is smooth. The pharynx is 7 mm. long, 4 mm. broad. The radula (Fig. 84) is white with a slight yellowish hue, unfolded 6.3 mm. long and about 4.2 mm. broad. It contains 45 rows with 85 teeth in each half row. The innermost tooth is a little simpler than the other lateral teeth, since its shaft does not overtop the cusp as in these. This tooth is 112 micra high, the second 126, the third 140 micra, the size increasing outwards to 220 micra. The five outermost teeth decrease from 190 to 170, 120, 80 and 50 micra. The two or three marginal teeth are rudimentary and nearly without cusp.

The salivary glands (*s*) of the present slug were asymmetrical (see Odhner, 1934, p. 269), the right gland broad and very short, the left is long and band-like and thickened distally. The oesophagus (*o*) begins with a spacious crop-like dilatation (*oi*) and goes from left to right, first anteriorly, then backwards and downwards, and enters the stomach from behind and below. This thin-walled part of the alimentary tract receives the muscular caecum (*c*) and the hepatic ducts (*l*). It is covered by the following, much more voluminous part, a gizzard (*k*), the triturating function of which is revealed by strong circular muscles and prominent ridges of the lining epithelium. The intestine (*i*) begins at the anterior end of the gizzard. The diameter of the intestine is the same for most of its course. It passes around the right side of the heart and then widens and opens in the mid-line among the branchiae on a low, strongly pigmented papilla.

Two brown, flat, blood glands lie over the oral tube, one in front of the central nervous system and the other behind it. The broad pericardium with the heart, and the kidney, are located as in other species. The hermaphrodite gland is coalesced

with the liver. The slender ampulla (*w*) is only a slight widening of the hermaphrodite duct. Where the ampulla ends, the male duct (*e*) communicates with a spherical prostate (*p*). It continues coiled and embedded in strong, longitudinal muscles (*z*) within a loose muscular sheath and passes with a small papilla into the terminal part, the so-called penis (*n*). The outer muscular sheath continues around the large tube, the wall of which is muscular and the epithelium cuticularized. The cuticle is 25–30 micra thick and forms salient plates of 0.4 mm. diameter in many places. Most of these plates bear a spine in the centre. These plates are evidently sometimes shed and renewed, since primordia (*y*) occur under the functioning ones. Close to the exit of the ejaculatory duct is an eosinophilous penial gland (*q*) as in *P. formosa* and *P. scabra* (White, 1950, figs 4, 15). The vagina (*v*), dorsally, the male aperture in the middle, and the oviduct ventrally, unite to a common tube, the genital atrium (*j*) which opens 7 mm. behind the right tentacle, between foot and hyponotum.

The vagina (*v*) is flattened dorsoventrally, broad, and strongly muscular. These muscles give the vagina a shining appearance in the dissected slug, and the cuticular plates make it hard. These plates measure up to 50 micra thick (Fig. 89) and bear spines about 0.7 mm. in diameter and up to 0.4 mm. high. They are periodically replaced like the penial ones. Further entally the vagina is narrow and ciliated and passes into the spherical spermatheca (*t*) which, because of its contents, is as dark as the blood glands and lies nearly in the mid-line behind the spermatocyst (*r*). The fertilizing or uterine duct (*u*) begins close to the entrance of the vagina, so that the seminal receptacles are rather semi-serial than serial. The uterine duct divides into a branch that enters the female gland mass (*h*) and another, the duct of the spermatocyst. The silken aspect of the latter is due to the sperms in it. The outlet of the oviduct (*ni*) is muscular.

Occurrence: Bahia (São Salvador), beach of Itapoã, 1 slug in tide pool on reef, December 1954; collected by Dr. Sebastian Gerlach (Kiel).

Further distribution: Virgin Islands, Antilles (typical material and var. *alaleta*); Jamaica (Haas, 1920, p. 142); Dry Tortugas, Florida (*Platydorís rubra* White, 1952).

Discussion of *Platydorís angustipes*.

The question whether the genus should be called *Argus* Bohadsch, 1761 (O'Donoghue, 1929, pp. 722–723; Thiele, 1931, p. 439) or *Platydorís* Bergh, 1877 was discussed by Engel (1934) and has been decided in favour of the new name by Opinion 185 of the International Commission on Nomenclature.

The preceding description contains only the characters of the available specimen, not those of Mörch's material (1863, p. 32) from St. Thomas (Antilles), that Bergh (1877*b*, p. 503) described with more details, and of *P. rubra* White (1952, p. 118) from Dry Tortugas. The latter was bright scarlet alive, the former had large vermilion blotches similar to those of *P. cruenta* (Q. & G.).

Number and size of the red flecks vary very much in *P. cruenta* (Bergh, 1905, p. 137; Eliot, 1910*a*, p. 426; Risbec, 1928, pp. 76, 80, pl. 1, fig. 7, pl. 2, fig. 7). *P. arrogans* Bergh (1877*b*, p. 513), a synonym of *cruenta* (*ibid.* 1890*a*, p. 912), has also a very variable extension of the red. Evidently Bergh himself did not consider the wavy denticulation of some marginal radular teeth in *arrogans* (1877*b*, p. 516) as a distinguishing character against *cruenta*. The aspect of the indentations on the outermost teeth in *P. angustipes* var. *alaleta* Bergh (1877*b*, pl. 58, figs 17, 18), one specimen of which is known from Sta. Cruz (Virgin Islands, near St. Thomas), gives the impression that these were somewhat worn; this variety does not deserve a separate denomination.

Comparison between Mörch's and Bergh's descriptions of *angustipes* with our slug shows almost complete agreement, and *rubra* White also seems to be conspecific. The breadth of the foot, it is true, is not indicated for *rubra*, but the term "rather

narrow" lets one suppose that it may be less than one-third of the foot-length as in *angustipes* and our slug. The height of the radular teeth in the latter falls between the shorter teeth of *rubra* and the longer ones of *angustipes*. Their number agrees in our slug and *rubra*; the smaller number in *angustipes* is not decisive, since it refers to the anterior part of the radula. A difference of degree exists with regard to the colour of the radula, very light yellowish-white in the present animal, pale straw-coloured in *rubra* and bright yellow in *angustipes*. The spicules of the latter are up to 0.6 mm. and in our slug up to 0.7 mm. long.

***Thecacera pennigera* (Montagu). (Figs 91–102.)**

The biggest of the present slugs measured up to 20 mm. in length alive; the height attained 5 mm. and the breadth 3 mm. The animals are very transparent with brownish viscera and more or less numerous, large, bright orange blotches on back and sides, the number of which is not correlated with the size of the slugs. There are many small, round, black spots between the orange ones and even on the sole; they also form a ring around the genital aperture, and some lie in the wall of the genital atrium. The Brazilian slugs do not attain the brightness of Alder & Hancock's figure (1855, Fam. 1, pl. 21a). The orange pigment appears as granulations in the epidermal cells of sections. The black spots are also preserved in alcohol.

The smooth body is high and slender with a long, pointed tail. The greatest breadth lies in front of or behind the middle. The sole is narrower than the body, grooved and slightly notched in front, and produced into tentacular points. Two bosses are located to the sides of the mouth, "that hardly deserve the name of tentacles" (Hoffmann, 1933, p. 233). Around the rhinophores, which bear about 8 oblique laminations (Alder & Hancock: 14), there are big, lobed sheaths that leave the inner side free. They are coloured like the rest of the body. Two smooth, peg-shaped appendages flanking the gills are also dotted with orange and black, as is the rhachis of the tripinnate gills. The gonopore is situated on a boss half way between rhinophore and gill on the right side, on the level of the pericardial prominence.

The spicules and their development were drawn by Alder & Hancock (1855, Fam. 1, pl. 21a, pl. 48, Suppl.). The spicules of the present material are similar but not quite like them (Fig. 94). The largest measure about 0.17 mm. in length and 25 micra in diameter.

The epidermis contains many cyanophilous glands, mainly in the rhinophore sheaths and the appendages, that both also lodge groups of sunken pink glands, clusters of cells with a big vacuole united by a tunic of muscular or connective tissue. The cyanophilous glands are also numerous on the whole length of the sole, especially

FIGURES 90–99.

Doris verrucosa Cuvier. (Fig. 90.)

FIG. 90.—Ventral view of anterior end of big and of small slug.

Thecacera pennigera (Mont.). (Figs. 91–99.)

FIG. 91.—Dorsal view of living slug.

FIG. 92.—Right side view of living specimen with very numerous orange and black spots.

FIG. 93.—Sketch of mating slugs.

FIG. 94.—Spicules.

FIG. 95.—Preparation of alimentary tract, seen from left side.

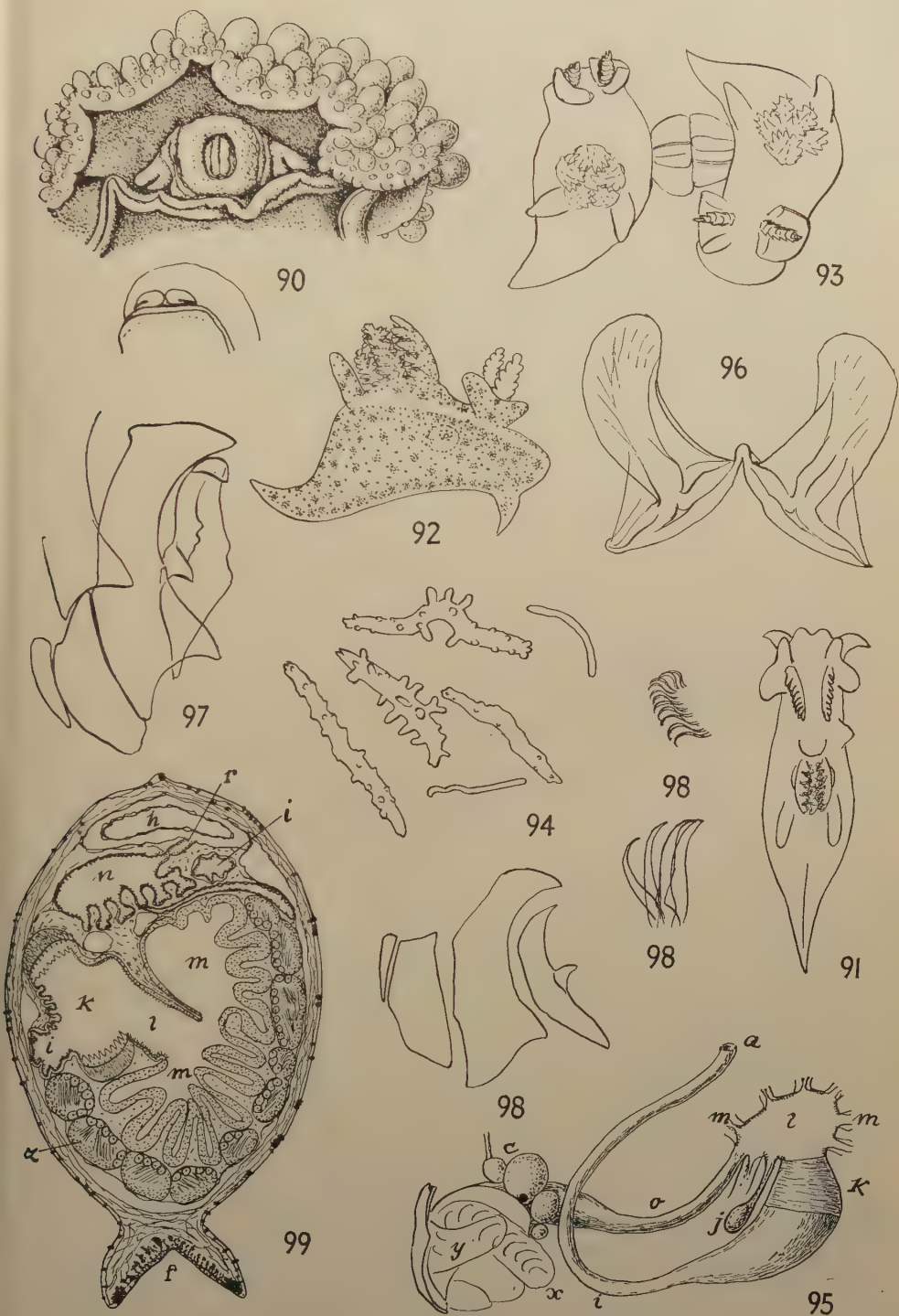
FIG. 96.—Jaws.

FIG. 97.—Half row of adult radula.

FIG. 98.—Preradula, young, and adult rows of radula of a 1.2-mm. long slug.

FIG. 99.—Transverse section on level of gizzard.

a—anus. c—brain. f—foot. h—heart. i—intestine. j—caecum. k—gizzard. l—stomach. m—liver. n—kidney. o—oesophagus. r—renopericardial communication. x—radula. y—jaw. z—ovotestis.



on its borders (Fig. 99). Every gill contains a number of small, round, compound branchial glands.

Around the cuticularized buccal cavity there are cyanophilous glands. Salivary ones were not seen. The jaw plates closely resemble those of *Polycera* with wing-like expansions (Odhner, 1941, figs 6, 7). The radula formula is $11 \times 2, 2, 0, 2, 2$. The innermost tooth is smaller (0.13 mm.) than the second (0.19 mm.), and bears a hook near its middle (Fig. 97). The second is the largest and has a hook at its base. The two outer teeth (0.1 mm. ; 50 micra) are flat, without hooks.

In the smallest slug (preserved 1.2 mm.) the radula is formed of three different types of teeth (Fig. 98). The oldest part consists of 10 rows of very thin hooks 2, 0, 2, of 13 to 18 micra length. This is the pre-radula (Pruvot-Fol, 1926). Then follow nine rows of an intermediate type, 40 micra long, 2, 2, 0, 2, 2, the two inner lateral teeth being stronger than the two marginal ones, and already resembling the adult shape. The transition of the form of the teeth is gradual ; the later ones of the second type are scale-shaped plates, not hooks. Thirdly there are eight rows of the adult shape, but still smaller, 0.12 mm. in maximum length. In a slug of 1.5 mm. length the radular teeth were nearly all of the adult type, only a small number retaining juvenile traces.

The ciliated oesophagus (*o*) enters the stomach (*l*) from the right side. The latter is ample and on all sides pierced by the openings of the multilobulate liver (*m*). The lumen of the liver contains only liquid, no solid food elements. The posterior part (*k*) of the stomach is surrounded by a belt of strong annular muscles and lined with cuticular cones on its epithelium cells. It contains solid food, chiefly avicularia of *Bugula turrita* (Des.), on which the slugs were found, and some diatoms. From the anterior limit of this gizzard arises a small, stalked caecum (*j*). The ciliated intestine (*i*) that continues the lumen of the gizzard narrows gradually and runs on the left side, passing over the oesophagus in front of the heart and turning backwards to the middle, where it ends among the gills (*a*).

The heart is located in a conspicuous pericardial prominence. In front of it lies a blood gland. The renopericardial duct (*r*) unites the lobed kidney (*n*) with the heart (*h*).

The protandric ovotestis (*z*) lies alongside the liver lobes (*m*). The follicles contain the male cells on the outer and the female ones on the inner wall. The hermaphrodite ducts (*g*) unite and form a spherical ampulla (*p*) which lies anteriorly on the underside of the genital mass. The spermoviduct (*q*) which leaves the ampulla passes through the folded female gland mass (*d*).

The male branch forms a thick, tubular prostate (*ro*), with big pink spheres of secretion in its epithelium, and continues as a shining, muscular vas deferens (*e*). The outer part of the latter, the ejaculatory duct (*ei*), is lined with cuticular teeth that dissolve in caustic potash. This duct is loosely surrounded by a sheath to which it is attached at its inner and outer end. The acrembolic copulatory organ opens into a spongy genital atrium (*ai*) which leads to the genital aperture (*os*). During mating the atrium is everted (Fig. 93).

The female branch, the oviduct, passes into the female gland mass which is connected (*w*) with the atrium too. From the latter arises the vagina (*v*) with a folded epithelium and therefore a star-shaped lumen in sections. It runs forward and widens to a spermatheca (*t*) lying towards the dorsal side. Out of the stalk of the spermatheca a coiling fertilizing duct (*u*) goes to the spermatocyst (*s*), continues to a fertilization chamber (*b*), filled with sperm, and ends in the female gland mass. The ciliated part of the oviduct is firmly coherent, while the glandular folds can easily be detached. The spawn is a 3 to 4 mm. long band of about 1.2 mm. breadth with truncate ends.

It is characteristic of these slugs that they react to unfavourable conditions, e.g., handling, keeping in a small bowl, adding of anaesthetic, etc., by decreasing in size. They contract, give off water, and thereby their body wall becomes less transparent.

The loss may attain about one-third of the body length. The heart beats 100 times a minute at about 22° C.

Occurrence : Near Ubatuba, north-eastern coast of the State of S. Paulo, on algae and Bryozoa, *Bugula turrita* (Des.), in the lower tidal zone, December 1954, July and September 1955, hundreds of slugs of all sizes. Enseada de Guarujá on the island of S. Amaro, near Santos, 1 animal, 30 November 1955.

Further distribution : European Atlantic coasts, England (Alder & Hancock, 1854, Genus 5 : 1855, Fam. 1, plate 21a), France (Cuénot, 1927, p. 267) ; always rare and therefore not known with respect to its genital organs (Odhner, 1941, p. 11). Mediterranean, Sicily (Vayssière, 1913, p. 339).

Discussion of *Thecacera pennigera*.

Bergh (1892a, p. 1141) and Pruvot-Fol (1950, p. 48) list the known species of *Thecacera*. *T. velox* Cockerell, 1901 was transferred to *Drepania* by MacFarland (1929), now *Trapania* Pruvot-Fol (1931, p. 309).

As far as I have seen none of the descriptions mentions a posterior gizzard, as Hoffmann (1938, p. 1090) called such structures. *Goniodoris* (Forrest, 1953, p. 234 ; Marcus, 1955, fig. 207) and *Corambella carambola* Marc. have a posterior gizzard too ; our species of *Polycera*, *Polycerella*, *Okenia*, and *Glossodoris* have not.

Already Eliot (1910, p. 153) mentioned hooked spines of the ejaculatory duct (or penis) in the generic diagnosis, since he had found such armature in his *T. maculata* from the Indian Ocean.

Polycerella conyna, sp. nov. (Figs 104–110.)

The two living slugs were 2.5 to 3 mm. long and 1 mm. high ; the preserved animals measure : length 1.7 mm., breadth 0.5 mm., height 0.7 to 1 mm. Alive they were rather transparent with brownish viscera and black and white spots in the skin. The foot, especially its hind end, is white, due to numerous glands (*x*) that are brilliantly white.

The back is high and the sole narrow ; the anterior angles of the foot (*ai*) are prolonged. Beside the mouth there are two small knobs, too short to be called labial tentacles. The rhinophores are slender, blunt and about 0.5 mm. long, without sheath, folds or perfoliations. From the mouth a ridge extends backwards on both sides and runs out on the level of the genital apertures (*r*) ; it represents the pallial ridge (*zi*). On the sides there is a number of more or less symmetrical small knobs, one or two pairs beside the pericardial prominence (*z*), one on the level of the anal opening, and two or three farther behind. Between these and nearer to the mid-line there stand two pairs of larger appendages, the anterior 0.2 mm. long, the posterior 80 micra.

The three gills (*g*) are simply pinnate and not webbed ; at their bases are two branchial glands (*b*) composed of ciliated cells with big nuclei, known in many Doriadacea (Hoffmann, 1940, p. 48). The foot is provided with numerous big cyanophilous glands (*x*) along its whole length. The papillae (*y*) on the notum contain large unicellular cyanophilous epidermal glands which also occur in the rest of the skin. The animals were preserved in "Susa", so that the spicules were dissolved.

In our sections the pharyngeal cavity is not visibly cuticularized. The extremely delicate radula has the formula 2, 1, 0, 1, 2. The strong lateral teeth (height 20 micra) have three cusps, the two terminal of which are united by a membrane ; the third, half down the shaft, is smaller. The marginal teeth (12 micra) have long, sickle-shaped cusps and triangular bases that overlap. The salivary glands are very small, 40 micra long, smaller than in *P. emertoni* (Bergh, 1883, pl. 9, fig. 4, a). The stomach (*e*) is large. On the left side, beside the outgoing intestine (*i*) is a small spherical caecum (*c*) which contains a ball of muscle fibres from the principal food of *P. conyna*, the ctenostomatous bryozoan *Amathia distans* Bsk.

The three principal parts of the liver (*m*) are lobed and lined with high club-shaped cells with distinct walls. In the hepatic lumen and also inside the cells some food

particles are recognizable, the characteristic cuticular teeth of the gizzard of *A. distans* which is frequent at the locality where *P. conyna* was taken. The intestine (*i*) runs forward and bends to the right side at the level of the genital opening. Then it turns backwards and opens behind the gills, near the middle of the body. The renal pore lies immediately in front of the anal opening.

The lobes of the ovotestis (*ze*) wrap round the liver. The follicles appear to produce either eggs, near to the liver, or sperm, farther outside. The male follicles are fewer and larger. The ducts from the hermaphrodite gland unite and form a narrow ampulla (*a*) that continues as spermoviduct (*h*). The male branch (*d*) widens and curves, and its epithelium becomes high and prostatic (*p*). This glandular part is 0.45 mm. long from tip to tip, and about 0.10 mm. in diameter. The following portion, the ejaculatory duct, is 0.25 mm. long, 40 micra in diameter, muscular, and densely ciliated. The muscle sheath continues, and the male duct passes for 0.12 mm. through a space where it is not connected with the muscular sheath. This part is the eversible, acrembolic penis (*q*), the outer half of which is provided with cuticular spines.

The female branch, the oviduct (*o*), enters a small fertilization chamber (*f*) from which it opens into the albumen lobe (*k*) of the female gland mass. A short fertilizing duct (*u*) connects the fertilization chamber with the canal (*sc*) of the spermatocyst; the ectal opening of the duct is provided with a strong sphincter. From the albumen gland the oviduct continues as a thin ciliated tube with cyanophil glands and leads to the folded mucus gland (*l*). From the end of the latter several connections pass through the "female vestibulum" (Pohl, 1905) to the female atrium that opens 0.1 mm. behind the common male and vaginal aperture.

The penis ends in a pouch 80 micra deep which opens with the male pore. Dorsal to the penis a short muscular canal leaves the pouch and forms a wide (0.21 mm.), ciliated sac (*ve*), the entrance of the vagina (*v*). The vagina runs backwards, gives off the canal (*sc*) of the spherical spermatocyst (*s*), the diameter of which is 0.12 mm., and ends in a pear-shaped spermatheca (*t*) 0.2 mm. long. The arrangement of the seminal receptacles (*s*, *t*) is of the semi-serial type as in *Polycera*.

FIGURES 100-110.

Thecacera pennigera (Mont.). (Figs 100-102.)

FIG. 100.—Diagram of reproductive organs.

FIG. 101.—Transverse section of ejaculatory duct.

FIG. 102.—Longitudinal section of same.

ai—genital atrium. *b*—fertilization chamber. *d*—female gland mass. *e*—vas deferens. *ei*—ejaculatory duct. *g*—hermaphrodite ducts. *os*—genital aperture. *p*—ampulla. *q*—spermoviduct. *ro*—prostate. *s*—spermatocyst. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—oviduct (nidamental duct).

FIG. 103.—*Polycerella emertoni* Verr., drawn after Verrill's description.

Polycerella conyna, sp. nov. (Figs 104-110.)

FIG. 104.—Dorsal view of living slug.

FIG. 105.—Right side view of same.

FIG. 106.—Lateral teeth of radula.

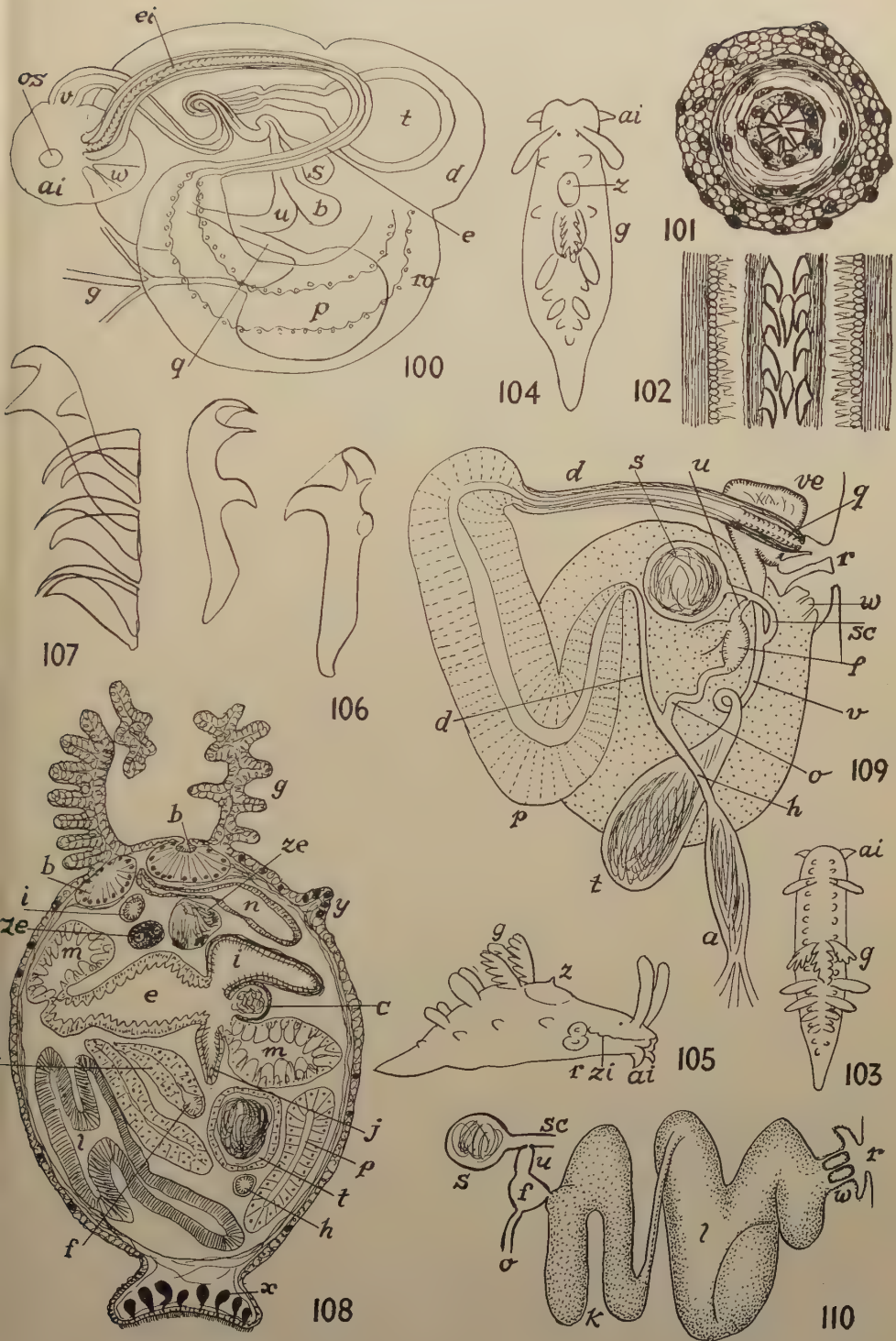
FIG. 107.—Marginal teeth and one lateral tooth of radula.

FIG. 108.—Combined transverse section on level of gills.

FIG. 109.—Reconstruction of genital organs.

FIG. 110.—Reconstruction of female gland mass unravelled.

a—ampulla. *ai*—angles of foot. *b*—branchial gland. *c*—caecum. *d*—vas deferens and ejaculatory duct. *e*—stomach. *f*—fertilization chamber. *g*—gill. *h*—spermoviduct. *i*—intestine. *j*—oesophagus. *k*—albumen gland. *l*—mucus gland. *m*—liver. *n*—kidney. *o*—oviduct. *p*—prostatic part of male duct. *q*—penis. *r*—genital apertures. *s*—spermatocyst. *sc*—canal (stalk) of spermatocyst. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina (and spermathecal canal). *ve*—entrance of vagina. *w*—female vestibulum. *x*—foot gland. *y*—notum papilla. *z*—pericardial prominence. *ze*—ovotestis. *zi*—pallial ridge.



Occurrence : Ubatuba, northern coast of the State of São Paulo. Among algae from the lower tidal zone. Two specimens in December 1954.

Discussion of *Polycerella conyna*.

The two previous species of *Polycerella* are *P. emertoni* Verrill (1881, p. 387) and *P. davenporti* Balch (1899, p. 150), both from the north-eastern coast of the United States. The radulae of these two species (Bergh, 1883, pl. 9, figs 5, 6 ; Balch, 1899, pl. 1, figs 1, 2) are similar and hardly distinguishable from that of *conyna*. As the dorsal papillae of *P. emertoni* were not figured, we made a drawing of them (Fig. 103) based on Verrill's description ; they are a little different from our species. *P. davenporti* has only small papillae, one pair in front of, one beside, one behind the gills. and two very small pairs forming a rosette still farther back. The gills of *P. davenporti* are webbed. From the description of Bergh's dissected *P. emertoni* differences in the reproductive organs also emerge. The efferent duct of *P. emertoni* is nearly twice as long as the prostate, and the spermatocyst is pear-shaped.

Polycerella zoobotryon Smallwood (1910, p. 143) from the Bermuda Islands belongs to the Phanerobranchiata Suctorina and constitutes the type of the genus *Bermudella* Odhner, 1941 (p. 15) in the family Goniodorididae.

Polycera aurisula, sp. nov. (Figs 111–119.)

The present slugs are all young. Alive and creeping four of them are no more than 3 mm. long, 0.6 mm. broad, and 0.8 mm. high. A fifth specimen (Fig. 113) is about 6 mm. long, but its genital organs are only just beginning to develop. The colour is a soft brown, mottled all over the back, somewhat more concentrated in front of and between the rhinophores, on the sides of the prebranchial part of the body and around the gills. The velar processes have an orange base, a blue middle zone and a light blue tip. The extrabranchial appendages have a blue ring in the middle followed by a yellowish orange one and a light tip. A triangular spot of blue and orange, though paler, occurs on the tail. All colours persist in alcohol.

The velum has four, in the biggest slug six, slender, digitiform, pointed processes. The pallial ridge that includes the rhinophores bears few broadly interspaced tubercles in front of and behind the gills, and continues as a crest on to the pointed ending tail. The gills are flanked by three thick, carrot-shaped appendages on each side, the length of which increases from the anterior to the posterior one. The rhinophores have, as sections show, nine closely-set lamellae and a narrow, longish distal knob,

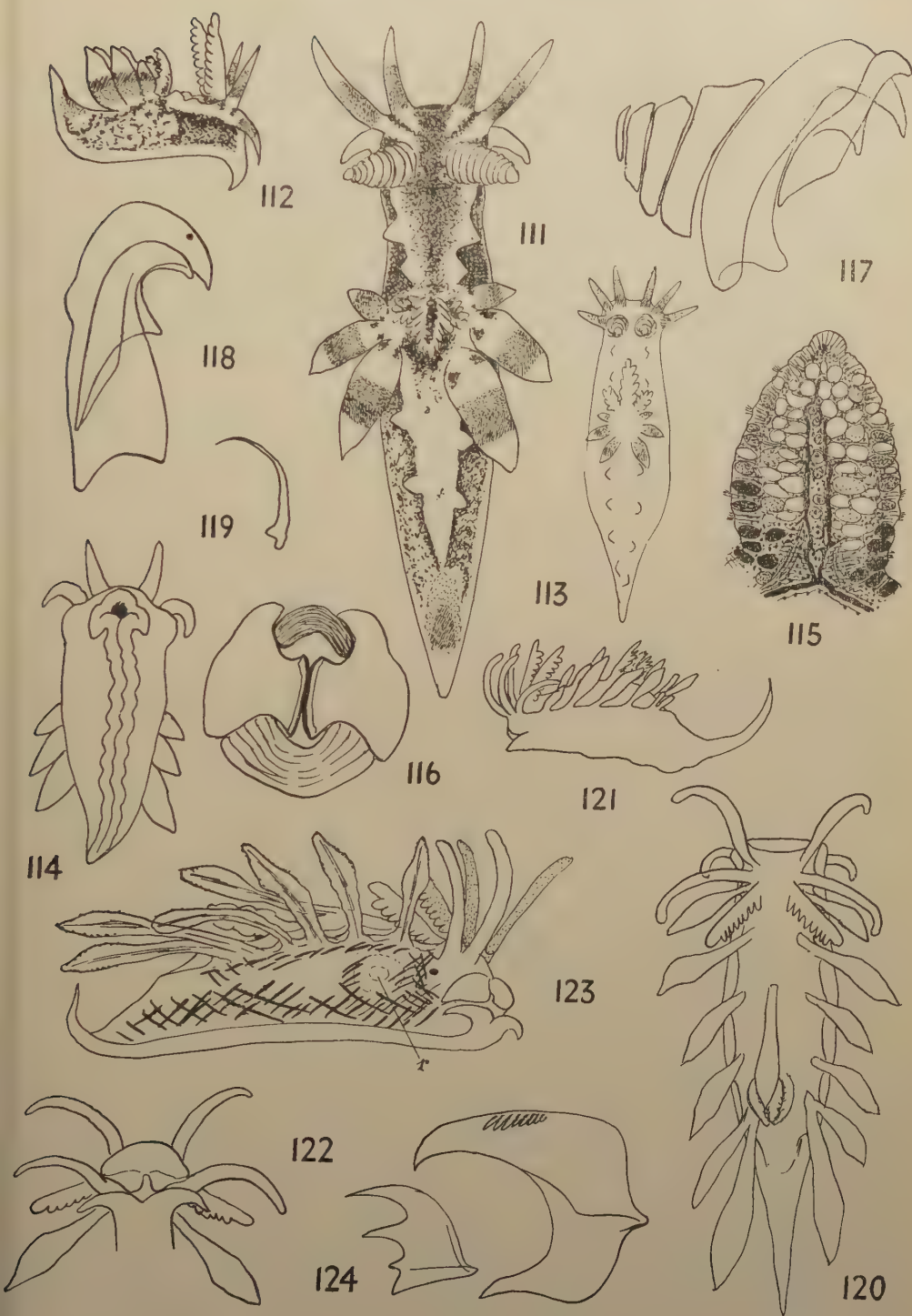
FIGURES 111–124.

Polycera aurisula, sp. nov. (Figs 111–119.)

- Fig. 111.—Dorsal view of 3-mm.-long living slug. Stipples for blue, streaks for orange, speckles for brown.
 Fig. 112.—Lateral view of living animal.
 Fig. 113.—6 mm. long slug.
 Fig. 114.—Ventral view of preserved slug.
 Fig. 115.—Section of extrabranchial appendage.
 Fig. 116.—Jaws.
 Fig. 117.—Half row of radula.
 Fig. 118.—Other aspect of first and second inner tooth.
 Fig. 119.—Preradular tooth.

Okenia impexa, sp. nov. (Figs 120–124.)

- Fig. 120.—Living slug in dorsal view.
 Fig. 121.—Same in lateral view.
 Fig. 122.—Fore end of same in ventral view.
 Fig. 123.—Lateral view of preserved specimen with spicules.
 Fig. 124.—Half row of radula.



There are no oral tentacles. The gills are three in number, one big anterior and two small lateral ones.

The narrow foot has projecting margins ; its frontal end has long produced slender corners and is not transversely grooved. The rather soft (Bergh, 1880, p. 606) spicules that occur all over the body are all monaxonous and have sometimes a rough surface. The biggest of them are 0.3 to 0.4 mm. long and 35 micra in diameter.

The yellow jaws have delicate wing-like processes and strong inner borders 0.18 mm. long. The compressed radula is 0.43 mm. long, 0.18 mm. broad. Its formula is $9 \times 4, 1, 1, 0, 1, 1, 4$. The innermost or first tooth is two-thirds as long (90 micra) as the second (135 micra) and has a spur in its middle. The second, the largest of the row, has a basal spur, more adequately described as a prolonged angle. The four outer teeth diminish, from the first which is 60 micra high and 17 micra broad to the outermost which is 32 micra high and 2 micra broad. In front of the radula is a number, about ten on each side, of preradular teeth that are curved needles with a broadened base, resembling those of *P. quadrilineata* (Pruvot-Fol, 1926, fig. XIII, p. 250).

The extrabranchial papillae are covered with superficial gland cells that are cyanophilous at the base of the papilla, erythrophilous in the middle, and do not stain in the tip. The interior of these appendages contains a great number of faintly staining vesicular cells, probably of supporting function, and a central blood vessel forming a loop.

Occurrence : Island of São Sebastião, among algae, chiefly Padina, grown on stones in the upper littoral ; 4 specimens in April 1954. Ubatuba, about 80 km. north-east of the first locality, among algae ; one specimen in December 1954.

Discussion of *Polycera aurisula*.

The present species is very closely related to or perhaps even identical with *Polycera hummi* Abbott, 1952, known from the southern Atlantic coast of the United States (North Carolina to Florida). The extrabranchial processes of *hummi* differ in shape from those of *aurisula*. None of the 6 specimens of *hummi*, all considerably larger than the present slugs of *aurisula*, has more than four frontal processes. On the other hand the rhinophores of *hummi* have 13 or 14 lamellae against 9 in *aurisula*. The only character that really separates the Brazilian material from the North American species are five denticles on the innermost marginal radular tooth of *hummi*.

In Odhner's key (1941, pp. 16-19) *P. zosteræ* O'Donoghue (1924, p. 7) comes nearest to our species. It differs from *P. aurisula* by rhinophoral stalks that occupy about half the length of the rhinophores, club-shaped with 6 shallow leaves, back and sides of the body covered with tubercles, and digitiform extrabranchial appendages. Some species described since Odhner's synopsis were recently mentioned (Marcus, 1955). None of them needs comparison with *aurisula*.

Okenia (Okenia) impexa, sp. nov. (Figs 120-127.)

The biggest of the six available slugs was 7 mm. long alive and 1 mm. broad. Another preserved slug was 3 mm. long, 1 mm. high and 0.8 mm. broad. The animals are white and have a net of superficial brown pigment forming patches on the back. The tips of the dorsal papillae are light yellow ; the anterior border of the head is yellow, the foot white.

The body is broad in front, pointed behind, with a tail that measured 1 to 1.5 mm. in the living slug. The foot is narrower than the body, its sole flat, its lateral borders salient, and its simple anterior margin is notched in the middle. The front angles are produced and pointed. The flat back is smooth except for one papilla in the middle, about half-way between rhinophores and gills. The pallial ridge on each side bears 6 to 8 claviform, though pointed, rather stiff appendages, about 0.8 mm. in

length. They begin at the level of the rhinophores, continue at equal intervals and end behind the gills with a bifurcated papilla on each side, here counted as two appendages united at their bases. The branchiae are 0.4 to 0.5 mm. long, simply pinnate plumes. Immediately behind them the anus opens without a prominent papilla, on the surface of the back. The genital opening (*r*) lies on the level of the first right dorsolateral appendage.

In front the pallial ridge encloses two pairs of cylindrical filaments, 0.8 mm. long, that are curved in the living slugs. The anterior border of the notum is developed as a narrow frontal velum that is thickened on the sides of the mouth, thus forming short lobes, the labial tentacles. The 0.4 mm.-long rhinophores have about 9 leaves and are smooth at the base and at the tip.

The inner mouth is provided with a ring of muscles and with radiate fibres (Hoffmann, 1938, p. 966, fig. 664E), but has only a thin cuticle, no armature on the labial disc, neither in the typical form of a ring of hooklets (*Okenia*), the "anneau mandibulaire" of Vayssière, nor in that of two lateral hamate plates (*Idaliella*). The pharyngeal crop (Fig. 125, c) is not pedunculate, the salivary glands (*si*) are short sacs. The radula has the formula $17 \times 1, 1, 0, 1, 1$, and consists of a medial tooth 42 micra high and a marginal one 25 micra high (Fig. 124). The inner border of the larger, hook-shaped, tooth bears seven or eight denticles, the size of which decreases from the cusp backwards. The smaller tooth ends with a sharp cusp, and its edge has two secondary cusps, an upper, nearly as long as the principal cusp, and a lower, considerably smaller, though distinct point.

The lateral papillae contain a continuous axial bundle of spicules, and their epithelium is provided with some glands. The branchial glands reach farther distally than those of *Goniodoris castanea* (Hecht, 1895, pl. 5, figs 71-72). There are spicules in the rhachis of the gills as well as in the other parts of the body including the foot. The spicules are up to 420 micra long and 20 micra thick, but those in the dorsolateral appendages are much smaller. The stiffness of these papillae which contrasts with those of *O. leachii* (Alder & Hancock, 1855, Fam. 1, pl. 27, fig. 6) is probably due to their axis of spicules.

The central nervous system resembles that of *Goniodoris nodosa* (Mont.) studied by Pelseeneer (see Pelseeneer, 1906, fig. 159; Hoffmann, 1936, fig. 553B). Cerebral and pleural ganglia are completely fused without an external furrow between them. The subcerebral commissure discussed by Hoffmann (loc. cit., p. 798) is distinct and thicker than the visceral loop. The latter contains an abdominal ganglion immediately behind the right cerebropleural ganglion.

The ovotestis contains male cells in a central cavity and female ones in the surrounding follicles as in the following species (Fig. 16). The hermaphrodite duct (*h*) enters a globular ampulla (*a*). The spermoviduct (*x*) gives origin to a short oviduct (*o*) which opens into the female gland mass (*g*), and to the vas deferens. Immediately behind the bifurcation the latter forms a long simple prostatic tube (*q*).

The emerging male duct (*e*) continues thin and winding. Farther outwards its muscle layer increases, and the lumen of the outermost part is lined by cuticular spines (Fig. 127). This thickened external part, the penis (*p*), is 0.3 mm. long. The pointed spines are arranged in about 25 rings of six spines each, and their length increases from 3 to 20 micra towards the tip in everted condition. A very small papilla of the acrembolic copulatory organ projects into the male atrium (*m*).

From the vagina (*v*) a short channel leads to the voluminous spermatheca (*t*) that is full of sperm in the slug, the reproductive organs of which were reconstructed in Fig. 126. The duct to the spermatocyst (*s*) is longer, and this vesicle is short and empty in the same specimen. The arrangement of the seminal vesicles is of the vaginal type. The fertilizing duct (*u*) debouches into the female gland mass (*g*) through the oviduct (*o*). The oviducal opening (*n*) lies near that of the vagina.

Occurrence: (1) Island of São Sebastião, among algae on boulders in the upper littoral, 2 specimens, June 1953 and April 1954. (2) Guarujá, 10 km. east of Santos,

1 slug, July 1954. (3) Bay of Santos, Ilha Porchat, 1 animal, September 1954. The 2 latter biotopes are similar to the first, but much more exposed. (4) Near Ubatuba, 2 slugs, July 1955, among algae in a sheltered bay.

Discussion of *Okenia* (*Okenia*) *impexa*.

The genus *Okenia* Menke, 1830 (Bronn, 1826 : *nomen nudum*), the name of which takes the place of the preoccupied *Idalia* Leuckart, 1828, comprises species with appendages in the middle of the back and others without them. Bergh (1881, p. 144) called the first group *Idalia* (proprie) and the second (p. 145) *Idaliella*. The two sections are to-day considered as subgenera, the first of which followed the alteration of the generic name. Bergh's second character, the labial armature developed as a ring of hooks in *Okenia* and as hamate lateral plates in *Idaliella*, must be abandoned, since the 2 narrow bands of scale-like elements in *Okenia echinata* Baba contrast with the *Okenia*-like papillae in the median part of the back, and the present species has no labial armature.

The species generally recognized as valid are :

- (1) *Okenia* (*Okenia*) *elegans* (Leuckart, 1828). Alder & Hancock, 1855, p. 46, Fam. 1, pl. 27, figs 1-4. Bergh, 1881, pp. 146-178 ; 1883, pl. 6, figs 1-9, pl. 7, figs. 1-3. Vayssière, 1913, p. 354. Pruvot-Fol, 1954, p. 308.
- (1a) *O.* (*O.*) *elegans* var *dautzenbergi* (Vayssière, 1919, p. 76). Vayssière, 1930, *Faune de la Méditerranée*, *Idalia elegans et sa variété Dautzenbergi*. Pruvot-Fol, 1954, p. 310.
- (2) *O.* (*O.*) *cirrigeria* (Philippi, 1839). Vayssière (1913, p. 354) maintains this species and *O. leachii* separated, Bergh (1881, p. 144) approached them to one another.
- (3) *O.* (*Idaliella*) *aspersa* (Alder & Hancock, 1845, Fam. 1, pl. 26). *Ibid.* 1855, p. 46, pl. 46, Suppl., fig. 24, App. p. IV. Vayssière, 1913, p. 356. Pruvot-Fol, 1954, fig. 121m.
- (4) *O.* (*I.*) *inaequalis* (Forbes & Hanley, 1853). Alder & Hancock, 1855, p. 46, App. p. V. Perhaps merely a variety of *aspersa* (Eliot, 1910, p. 159).

FIGURES 125-136.

Okenia impexa, sp. nov. (Figs 125-127.)

Fig. 125.—Side view of dissected alimentary tract.

Fig. 126.—Diagram of reproductive organs.

Fig. 127.—Introverted penis.

Okenia evelinae, sp. nov. (Figs 128-136.)

Fig. 128.—Dorsal view of living slug.

Fig. 129.—Ventral view of same.

Fig. 130.—Head of preserved animal from below.

Fig. 131.—Spicules.

Fig. 132.—Teeth of radula.

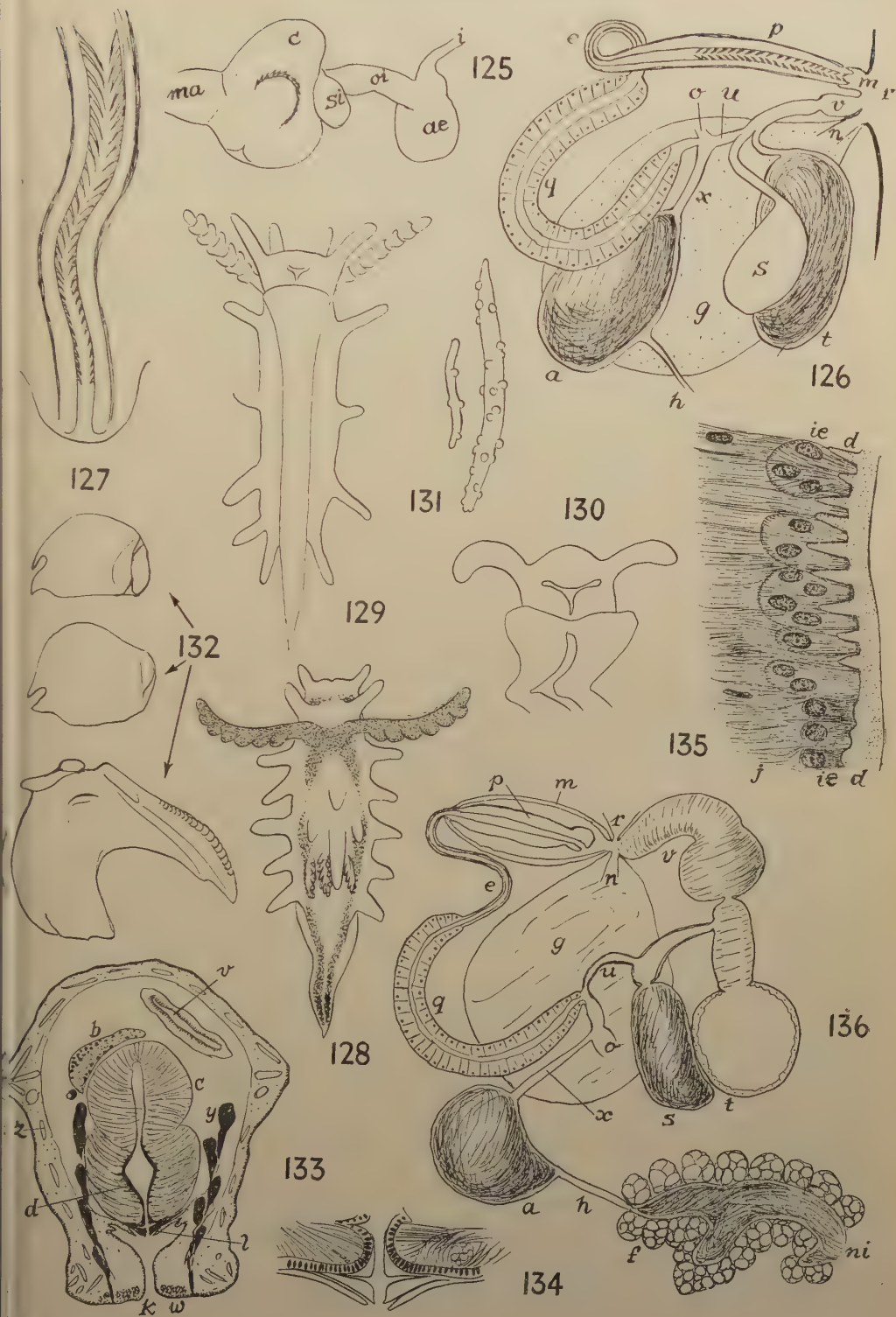
Fig. 133.—Combined section showing outer and inner mouth.

Fig. 134.—Inner lips.

Fig. 135.—Cuticle of entrance to pharyngeal cavity.

Fig. 136.—Diagram of reproductive organs.

a—ampulla. *ae*—stomach. *b*—brain. *c*—crop (buccal pump). *d*—cuticle of entrance to pharyngeal cavity. *e*—vas deferens. *f*—female follicles. *g*—female gland mass. *h*—hermaphrodite duct. *i*—intestine. *ie*—epithelium of pharyngeal cavity. *j*—muscles of pharyngeal cavity. *k*—outer mouth. *l*—labial beak. *m*—male vestibule. *ma*—mouth cavity. *n*—nidamental opening. *ni*—male part of ovotestis. *o*—oviduct. *oi*—oesophagus. *p*—penis. *q*—prostatic duct. *r*—genital aperture. *s*—spermatocyst. *si*—salivary oviduct. gland. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—oral sensory cells. *x*—sperm-oviduct. *y*—labial glands. *z*—spicules.



- (5) *O. (O.) leachii* (Alder & Hancock 1854a, p. 103). Ibid. 1855, p. 46, Fam. I, pl. 27, fig. 5, pl. 46, Suppl., fig. 23. Vayssière, 1913, p. 354. Pruvot-Fol, 1954, p. 309.
 - (6) *O. (I.) pulchella* (Alder & Hancock, 1855, p. 46, App. p. V). Vayssière, 1913, p. 355. Pruvot-Fol, 1954, p. 311.
 - (6a) *O. (I.) pulchella* var. *fusca* (Odhner, 1907, p. 101).
- Notes on the radula of *elegans*, *inaequalis*, and *pulchella* were given by Alder & Hancock, 1855 on the third and fourth of the unnumbered pages that contain the text to pl. 46, Supplementary.
- (7) *O. (O.) tentaculata* (Stimpson, 1855, p. 379). Bergh, 1881, p. 144. Baba, 1949, p. 138. Two frontal cirri.
 - (8) *O. (O.) mediterranea* (Ihering, 1886, p. 39). Vayssière, 1913, p. 355. Pruvot-Fol, 1951, p. 29. Similar to *O. amoenula* (Bgh.) (Pruvot-Fol, 1954, p. 311).
 - (9) *O. (O.) plebeia* (Bergh, 1902, p. 186). Baba, 1949, p. 138.
 - (10) *O. (I.) amoenula* (Bergh, 1907, p. 80). Barnard, 1927, p. 197.
 - (11) *O. (O.) vancouverensis* (O'Donoghue, 1921, p. 177).
 - (12) *O. (I.) barnardi* Baba (1937a, p. 295).
 - (13) *O. (O.) distincta* Baba (1940, p. 104). Radula somewhat similar to that of *impexa*, but papillae quite different.
 - (14) *O. (O.) japonica* Baba (1949, p. 45, 138).
 - (15) *O. (O.) echinata* Baba (1949, p. 46, 138).

Doris quadricornis Montagu, 1815 is an "obscure species" (Alder & Hancock, 1855, App. p. V-VI) that "can hardly be identified" (Eliot, 1910, p. 159). Bergh (1881, p. 145, note) thought that it will never be classifiable; he approached it to *inaequalis*. O'Donoghue (1929a, p. 777) replaced *elegans* Leuckart by *quadricornis* Montagu, and Pruvot-Fol (1953, p. 83; 1954, p. 310) united the latter with *aspersa*.

O. (O.) impexa is principally characterized by the marginal tooth of the radula, the very strong distal point of which as well as the 2 prominent cusps in the middle are really peculiar in *Okenia*. The aberrant outer teeth of *O. amoenula* (Bergh, 1907, pl. 13, fig. 10), *O. vancouverensis* (O'Donoghue, 1921, pl. 8, fig. 22), and *O. distincta* Baba (1940, fig. 4b) show that the present species, too, can be included in *Okenia*. It is known from cryptobranchiate Doridacea that the labial armature is not always a safe generic character (Odhner, 1926, pp. 53, 79). Among the Phanerobranchiata, *Goniodoris glabra* Baba (1937a, p. 294) has a smooth labial cuticle, nevertheless it is included in a genus where hooks as labial armature are the rule.

Besides the specimen that served as basis for the description of the reproductive organs another slug was sectioned. This corresponds to the first with regard to the hermaphrodite gland and the female gland mass. The penis however is minute, perhaps temporarily reduced, and not connected with the prostate. The latter is inflated by masses of sperm and agrees with that in Vayssière's figure of *Okenia elegans* (1901, pl. 4, fig. 24). Except for the shape of the prostate and some details, e.g. the length of the duct between vagina and seminal receptacles, our first series is also consistent with Vayssière's statements. Bergh's second figure of the reproductive organs of *O. elegans* (1883, pl. 6, fig. 5) can be compared with ours too, though the spermoviduct and still more the oviduct are drawn much longer, perhaps in consequence of the emptiness of the ampulla. Bergh's first figure (1881, pl. 7, fig. 11) with an inner lobulate prostate and an ectal prostatic duct suggests the possibility that part of the liver was considered as inner prostate.

Okenia evelinae, sp. nov. (Figs 128-137.)

The biggest slug was 8 mm. long alive, about 2.5 mm. broad, and 2 mm. high. The maximum length of preserved animals was 5.5 mm.

The integument is white and contains refractive granules on the back. The tissues of the inner organs are yellow, the liver dark yellow. The dorsal appendages,

the gills, and the borders of the foot are pure white. The rhinophores are violet, and the same colour occurs on the sides, the tail, and in small quantities on the back of full-grown animals. It is preserved in "Susa" and alcohol.

The body is broad and obtuse and produced into a tail of one-third of the body length. The foot is narrow with a smooth anterior border and rounded, slightly projecting corners. It ends with a pointed tail. In front of the gill four dorsal papillae surround the pericardial prominence, two median ones and two lateral between them. One of the lateral papillae may be double. The pallial ridge has five or six blunt, peg-shaped appendages on each side. One pair of them stands in front of the rhinophores on the anterior border of the notum. The four or five lateral processes extend backwards to the level of the gills. Their number is not correlated with the size of the slug. The axis of the appendages contains spicules.

The branchiae are very variable, there are four, five or six unipinnate gills. Of these the two middle gills can be united at their base. Some slugs have three bipinnate gills, others five, partly unipinnate, partly bipinnate branchiae. The branchial glands, voluminous in *O. impea*, are very small in *O. evelinae*. The minute anal papilla is only a fold of the skin overlapping the anus from the front and lies between the gills; the renal pore is in front of the anus to the right.

Long clusters of labial glands (*y*) open on both sides of the outer mouth (*k*). The inner mouth is surrounded by a thick cuticle that projects with a kind of bilabiate beak (*l*) on each side (Figs 133-134). Its position corresponds to the semicircular labial armature of *O. barnardi* Baba, but it is not composed of closely-set hooks. Farther inwards the smooth cuticle of the entrance to the pharyngeal cavity (*d*) has small processes on its basal side (Fig. 135). The sessile pharyngeal crop (*c*) is large. Short, sac-shaped salivary glands open into the pharynx under the hind end of the crop.

The radula (Fig. 132) consists of about 28 rows of teeth (1, 1, 0, 1, 1). The inner tooth is up to 90 micra long. On its inner side it bears 15 to 17 denticles, of which those near the cusp are stronger than those near the base. A boss on the inner surface of this plate occurs occasionally. The scale-shaped marginal tooth is about 40 micra long. It has one sharp point and farther below a second, less distinct one.

The oesophagus is strongly muscular and dilatable. The short, folded stomach contains several entire gizzards of *Amathia convoluta* Lmx. Numerous single gizzard teeth are lying within hepatic cells. The beginning of the gut has a typhlosole, it continues thin and straight. There is no caecum.

The central nervous system agrees with that of *O. impea*.

The spicules are up to 0.4 mm. long and 32 micra in diameter, slightly curved, pointed, and nodulous. The largest lie parallel along the pallial rim and the sides of the foot, small transverse ones occur in the rhinophores and the lateral margins of the sole. Perpendicular bundles support the tentacles, the sides of the notum, and the appendages.

The ovotestis forms a belt around the liver, enveloping it in the middle, not in front and behind. The gonad is a tube with transverse pouches, in which the male cells (*ni*) are located as well as in the central part. The numerous female follicles (*f*) accompany the male tube. The hermaphrodite duct (*h*) continues the central cavity of the ovotestis and forms a bean-shaped, almost globular ampulla (*a*). The spermoviduct (*x*) gives off the oviduct (*o*) and forms the prostatic part (*q*) of the male duct. The ectal part of the efferent duct (*e*) is ciliated and muscular. It enters the long penis (*p*) that lies within a spacious, folded vestibulum (*m*). This pleurembolic copulatory organ is 0.75 mm. long and 0.12 mm. in diameter. It is covered with a thin, smooth cuticle and lined with a ciliated epithelium (Fig. 137). The penis ends with a slight knob that has a subterminal orifice.

From the genital aperture (*r*), the common opening of the male atrium (*m*) and the broad oviduct (*n*), also a muscular vagina (*v*) leads inwards. Its dense annular muscle fibres give it a silky aspect in the dissected slug. Including its inner globular

dilatation the vagina is as long as the penis. The spermathecal duct is separated from the dilatation of the vagina and the spermathecal pouch by sphincters. The pouch contains no sperm in the specimens examined. Near the ectal sphincter the fertilizing duct goes out from the spermathecal duct and widens gradually towards the entrance of the spermatocyst (*s*). From this widening a thin ental part of the fertilizing duct (*u*) continues winding into the female gland mass (*g*). In the sausage-shaped spermatocyst spermatozoa are fastened to the wall with their heads.

Occurrence: Twenty-two slugs of various sizes on *Amathia convoluta* Lmx.; 14 km. west of Ubatuba in the lower tidal zone; July 1955. One specimen at Ilhabela, November 1955.

Discussion of *Okenia evelinae*.

Thiele (1931, p. 429) based the contradistinction of *Okenia* s. str. and *Idaliella* on Alder & Hancock's diagnoses of *Idalia elegans* and *I. aspersa* (1855, p. XVIII) and on Bergh's revision (1881, pp. 144-145; 1892a, pp. 1155-1156). It must however be restricted to "centre of back with (*Okenia*, s. str.) and without (*Idaliella*) filaments". The armature of the labial disc has already been discussed in the preceding species; and also the smooth beak of *O. evelinae* cannot be called a "spinous" (Alder & Hancock) or "hamate" (Bergh) ring. Further the lateral tooth of the radula is strongly denticulate in *O. evelinae*, though it belongs to the species with papillae on the dorsal surface. *O. japonica* has the same combination of characters of *Okenia* s. str. and of *Idaliella*.

A character which must be suppressed in the diagnosis of *Okenia* is that referring to indistinct tentacles. In the species nos. 12-15 of the preceding list, for example, as well as in *O. evelinae*, they are well developed and by no means "minute intumescences that hardly deserve the denomination of tentacles" (Hoffmann, 1933, p. 233). A massive prostate (Bergh, 1892a, p. 1149) besides a glandular prostatic part of the efferent duct (Bergh, 1881, pl. 7, fig. 11; 1902, pp. 188-189) cannot yet be considered as a safe generic character of *Okenia*. It is not shown in Bergh's second figure of *O. elegans* (1883, pl. 6, fig. 5), nor in Vayssière's drawing of the same species (1901, pl. 4, fig. 24), as little as in *O. impexa* and *O. evelinae*.

It is true that *O. evelinae* is not a typical *Okenia* with regard to its penis. An acrembolic efferent duct with cuticular hooks and muscular wall as in *O. impexa* seems indeed to be the typical male copulatory organ of *Okenia*. As far as I could consult the bibliography, penial hooks are indicated for *elegans*, *mediterranea*, *plebeia*, *amoenula*, and *vancouverensis*. The pleurembolic penis of the new species with "glans" and "preputium" in Bergh's terminology, differs fundamentally from the

FIGURES 137-145.

Okenia evelinae, sp. nov. (Fig. 137.)

FIG. 137.—Transverse section of penis.

Trapania maringa, sp. nov. (Figs 138-145.)

FIG. 138.—Living slug gliding on the surface of the water.

FIG. 139.—Same, side view.

FIG. 140.—Head of preserved slug.

FIG. 141.—Fore gut.

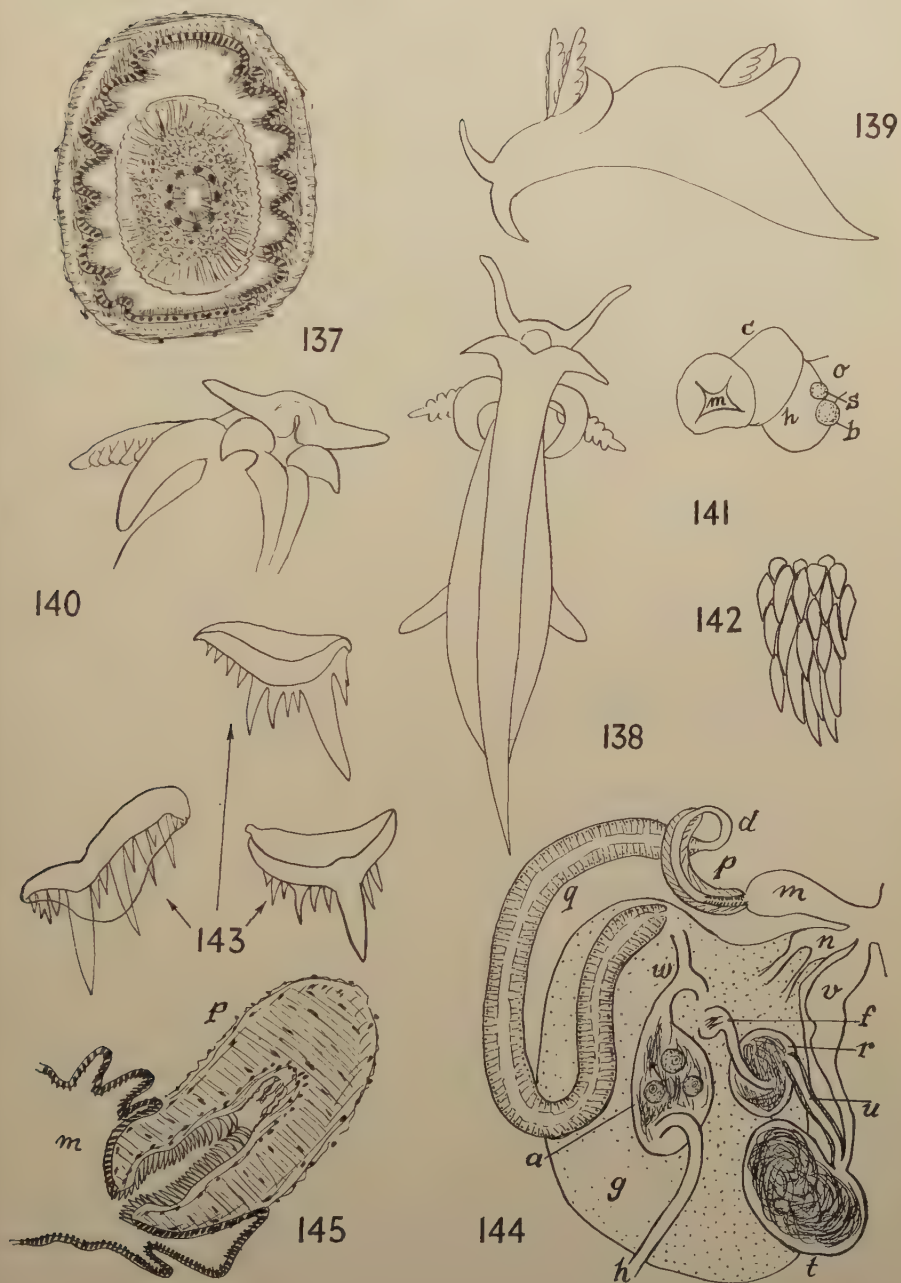
FIG. 142.—Labial armature.

FIG. 143.—Teeth of radula.

FIG. 144.—Diagram of reproductive organs.

FIG. 145.—Section of penis.

a—ampulla. *b*—buccal ganglia. *c*—crop. *d*—efferent duct. *f*—fertilization chamber. *g*—female gland mass. *h*—hermaphrodite duct. *m*—male atrium. *n*—nidamental duct. *o*—oesophagus. *p*—penis. *q*—prostatic part of vas deferens. *r*—spermatocyst. *s*—gastro-oesophageal ganglia. *t*—spermatheca. *u*—fertilizing duct. *v*—vagina. *w*—spermoviduct.



acrembolic organ of the other species. The semi-serial seminal receptacles of *O. evelinae* differ in degree from the vaginal ones in *elegans* and *impexa*.

All species of *Okenia*, the reproductive organs of which are known, were compared with *O. evelinae*; they, as well as all others, are distinguished by the combined characters of the gills, the marginal, and the dorsal appendages.

***Trapania maringa*, sp. nov. (Figs 138–145.)**

The living slugs were 6 to 7 mm. long, about 1.5 mm. of which belong to the tail. Preserved, they were 4.5 mm. long, 1.5 mm. high, and 1 mm. broad. The body is light and smooth. An irregular net of dark brown pigment, not found on the foot, gives the living animal a brownish hue. The pigment is lodged in the basal parts of the epidermal cells. It faded in alcohol. There is no notal ridge.

The tentacles are stout in the preserved (Fig. 140), more slender in the living animal (Fig. 138). The rhinophores bear six or seven leaves on their hinder side. The process at the base of the rhinophores is curved, thick, and more than 1 mm. long. The extrabranchial appendages that measure 1 mm. in length are strong. The three gills are bipinnate and have only few pinnules on their rhachis: the central branchia has seven on each side. At the bases of the gills are several well-developed branchial glands. The narrow foot is deeply sulcate along its middle and has strong tentacle-like anterior corners. The pedal glands are spherical and composed of several cyanophil cells each. In front there is a deep pouch with many blue glands. The mouth is surrounded by one superior and two lateral lobules.

The labial disc is covered by a reticulate cuticula, the meshes of which are prolonged into pointed pegs. The longest of these attain 25 micra. The radula has twenty or more pairs of teeth up to 60 micra broad. These are irregularly curved and bear a series of denticles. The five to twelve inner teeth are of very different size (6–14 micra). Outwards follows one cusp approximately 25 micra long and then one to four smaller marginal points, about 11 micra long. The crop (Fig. 141, *c*) is an insignificant, not pedunculate dilatation in front of the pharynx (*h*). The stomach contained coagulated juice and a copepod. It has no caecum.

The slug caught in September, though of the same size as that from July, was sexually mature in the female, that is, in advanced phase. The ovotestis lies for the most part behind the liver but extends also a little around it. The female cells are peripheral, and a few male elements, principally ripe spermatozoa, lie in the centre of the gonad. The ampulla (*a*) contains sperm and eggs. A wide but short spermoviduct (*w*) leaves the ampulla and enters the female gland mass (*g*) where it bifurcates.

The male branch is prostatic (*q*) in the greater part of its course which runs far backwards and then curves forward. A short, thin vas deferens (*d*) unites the prostatic part with the strongly muscular acrembolic penis (*p*). The penial epithelium is ciliated in its proximal (ental) part and cuticularized distally. The tip bears spines and ends at the bottom of the male atrium (*m*). The latter is folded in MacFarland's specimen of *T. velox* (Cockerell) and surrounds the "glans" as a "preputium" (MacFarland, 1929, pl. 35, fig. 13). The penis itself is not everted in MacFarland's slug.

The female gland mass (*g*) opens through several outlets (*n*) which lie ventrally to the male atrium. The vagina (*v*) begins as a wide and folded organ and continues entally as a narrower canal, MacFarland's vaginal duct. The voluminous spermatheca (*t*) is similar in *T. velox* and *T. maringa*, but the origin of the fertilizing duct is different. In *T. velox* it leaves independently beside the entrance of the vagina, so that the arrangement of the receptacles is serial. In *T. maringa* the ducts enter and leave the spermatheca on the same point. Thus these sacs are arranged semi-serially in *T. maringa*. The entrance and exit of the fertilizing ducts in the spermatocyst (*r*) also differ. These are united in *T. velox*, while the exit is independent in *T. maringa*, which is quite a rare feature. The fertilizing duct of the present species is uncommonly muscular in its course between the two seminal receptacles. The inner part, between spermatocyst and gland mass is thin and membranous. It contains sperm in the

sectioned slug. Before it debouches into the gland mass, it dilates and forms a fertilization chamber (f).

Occurrence: 2 slugs were obtained 14 km. west of Ubatuba among algae in the upper littoral, in July and September 1955.

Discussion of *Trapania maringa*.

The Genus *Drepania* was described by Lafont (1874), and Pruvot-Fol (1931, p. 309) introduced the modern name. The type species, *T. fusca*, came from Arcachon (Gironde). More than 50 years later a figure of *T. fusca* (Laf.) was published (Cuénot, 1927, fig. 1), but its radula is not yet known. Bergh (1892a, p. 1157) established the systematic position of *Trapania* among the Phanerobranchia Suctorioria.

The following are the recognizable species of *Trapania*. (1) *T. graeffei* (Bergh, 1881b, p. 636) from Trieste (loc. cit.) and Naples (Ihering, 1886, p. 37); (2) *T. tartanella* (Ihering, *ibid.*) from Naples; (3) *T. velox* (Cockerell, 1901) completely described by MacFarland (1929, pp. 485-496); (4) *T. japonica* (Baba, 1935, p. 336).

Bergh's specimen of *graeffei* and Ihering's of *tartanella* are both 7 mm. long alive. Their labial armatures do not agree completely. Pruvot-Fol (1954, p. 313) however considers both as synonyms of *fusca*. According to her, *tartanella* is a colourless young slug and *graeffei* a little older, slightly pigmented stage.

T. maringa differs from *velox* at first sight, as the Californian species is light grey with black longitudinal stripes and has orange tips on tentacles, rhinophores and foot corners. The radula tooth of *velox* and the two Mediterranean species ends with a strong hook, while the longest cusp of the radula in *maringa* is not the outermost. The other denticles of the tooth are nearly equal in size in *graeffei* and *tartanella*, so that it resembles a saw; this aspect is not consistent with the tooth of *maringa*.

The description of *T. japonica* Baba, 1935, was not available for comparison with *T. maringa*.

Dendrodoris atropos (Bergh). (Figs 146-154.)

Doriopsis atropos Bergh, 1879a, pp. 50-65.

The largest slug of our material (Fig. 146) was 12 cm. long, 7 cm. broad, and about 2 cm. high when alive. The smallest preserved specimen (Fig. 147) is 5 cm. long, measured over the curved back; 2.2 cm. broad, and 1.2 cm. high. The living animals are smooth with soft indistinct pustules on the notum. The skin of the preserved slugs is wrinkled, slightly convex between the folds, and so somewhat resembling seal leather. It does not contain any spicules. The strongly ruffled notal brim is 5 mm. broad on the sides in the living slug.

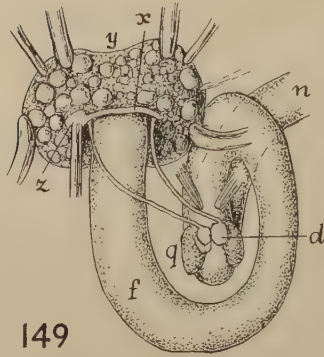
Only one of our five animals was seen in life; of the others three were received in formalin, one in alcohol. Therefore we give the colour of the living slug first. The notum was dark red with irregular black blotches and red, ruffled margin. The clubs of the rhinophores and the hinder side of their shaft were red, the anterior surface of the shaft was black. The gills were black with red tips and colourless efferent vessels. The anal papilla was black. The underside of the notal ruff was yellow, and this colour continued on to the upperside of the foot, where it showed some circular black and grey spots. The sole was yellow with confluent grey patches. The upper lip of the anterior border of the foot was red, the lower lip yellow.

The three slugs in formalin had been caught about 10 km. from our collecting place. Their colour was indicated as resembling our specimen; in one of them the black elements were nearly absent. On the other hand the small slug in alcohol is blackish-grey with a narrow light line around the notal brim, from which short stripes alternating lighter and darker go out.

The connective tissue on the inner surface of the body cavity, the so-called peritoneum, and that around all inner organs, is richly developed and is for the most part not pigmented. However the blood gland (*k*) and the surface of the oral tube,



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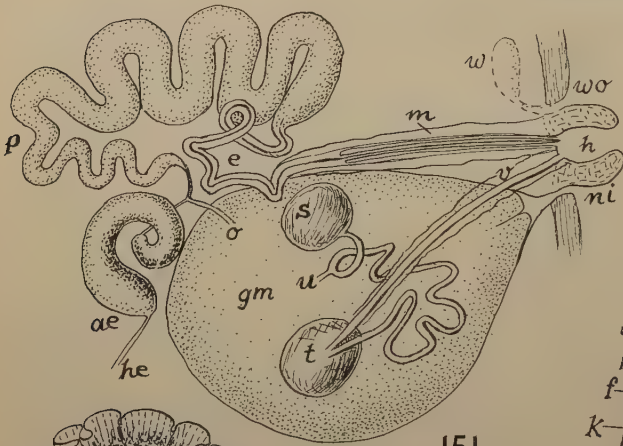
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148



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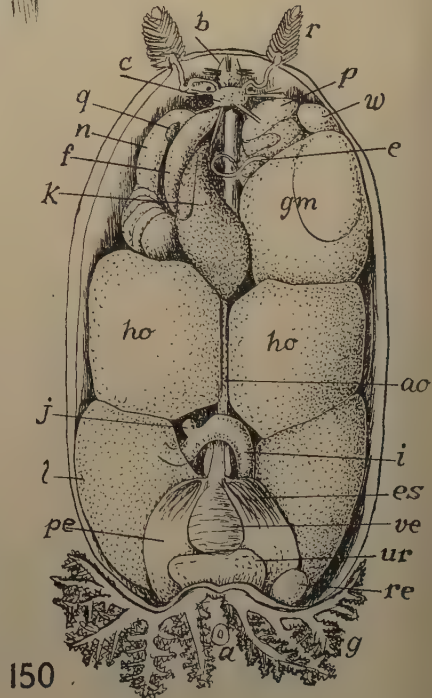
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154



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the gut, and the ectal parts of the genital ducts, penis, vagina, and nidamental duct, generally contain black granules. The black pigment is however not present in all these organs of the three dissected specimens. The different colours of the inner organs, viz. the orange of the brain and the renopericardial communication, the brilliant pink of the posterior gland of the oral tube, the oesophagus, and the prostate, the olive green of the surface of the liver, and the pink of the female gland mass certainly have no diagnostic value. In the specimen from alcohol only the black elements were to be seen. In the hepatic peritoneum whitish granules were observed that possibly are the corpuscles seen by Bergh (1879a, p. 57). They did however not react to hydrochloric acid.

The rhinophores (*r*) of the biggest slug, measured alive, were 8 mm. long. They have about thirty leaves. The rosette of the six tri- to quadripinnate gills (*g*) was 40 mm. in diameter. The anal papilla (*a*) lay slightly in front of the line that unites the bases of the third pair of gills. In the smallest preserved slug it appears a little farther behind. The foot may stand out backwards in the creeping slug. The anterior border of the foot is separated by a furrow into a lower and an upper lip. The first is entire, the second interrupted by the mouth pore. The minute tentacles (*te*) are connected with the upper lip. Between the border of the foot and the notum the larger genital papilla is situated on the right side in front.

The central nervous system (Figs 148–149) lies, as in the other species of the genus, in front of the pharynx (*f*) that is limited backwards by the salivary glands (*q*). The surface of the nervous mass is warty as in Hancock's figure (Hoffmann, 1936, fig. 560) of *D. denisoni* (for synonyms see Bergh, 1884, p. 694; Allan, 1947, p. 457) and in several other species of the genus. Only the abdominal ganglion (*z*) near the root of the visceral loop (*x*) is a little separated, but all other ganglia are completely coalesced. Even the pedal commissure (*y*), which is still recognizable in *D. denisoni* (Angas), is entirely concealed by nerve cells. In none of the many available descriptions of the central nervous system of *Dendrodoris* have we found so high a degree of concentration (see also Hoffmann, 1936, p. 799). The rhinophoral ganglia (*ri*), too, are hardly separated from the cerebropleural ganglia. One of the buccal ganglia (*d*) shows an indistinct group of special nerve cells, a vestigial gastro-oesophageal ganglion.

The blood gland (*k*), through which the aorta (*ao*) runs, is a flat organ located to the left over the stomach or to the right over the female gland mass. The heart (*ve*) is very big; the so-called pericardial gills (*es*), that are really pericardial glands

FIGURES 146–154.

Dendrodoris atropos (Bergh). (Figs 146–154.)

FIG. 146.—Dorsal view of living slug.

FIG. 147.—Ventral view of preserved slug.

FIG. 148.—Dorsal view of central nervous system.

FIG. 149.—Ventral view of brain and anterior part of intestine.

FIG. 150.—Inner organs, simplified.

FIG. 151.—Diagram of reproductive organs.

FIG. 152.—Penial papilla.

FIG. 153.—Transverse section of same.

FIG. 154.—Spines of same.

a—anal papilla. *ae*—ampulla. *ao*—aorta. *b*—oral tube. *c*—cerebropleural ganglia. *d*—buccal ganglia. *e*—vas deferens. *ei*—penial pouch. *es*—pericardial glands. *f*—pharynx. *g*—gills. *gm*—female gland mass. *h*—genital vestibule. *he*—hermaphrodite duct. *ho*—ovotestis. *i*—intestine. *j*—caecum. *k*—blood gland. *l*—liver. *m*—sheath of vas deferens. *mu*—muscles of vas deferens. *n*—oesophagus. *ni*—nidamental opening. *o*—oviduct. *p*—prostatic part of vas deferens. *pe*—pericardium. *q*—salivary glands. *r*—rhinophore. *re*—renopericardial duct. *ri*—rhinophoral ganglia. *s*—spermatocyst. *t*—spermatheca. *te*—tentacle. *u*—fertilizing duct. *ur*—auricle. *v*—vagina. *ve*—ventricle. *w*—vestibular gland. *wo*—opening of same. *x*—visceral loop. *y*—pedal commissure. *z*—abdominal ganglion.

(Hecht, 1895, p. 654 ; Hescheler, 1900, p. 343), are distinct on the anterior walls of the pericardium. The renopericardial communication (*re*) is globular.

The oral tube (*b*) with the united posterior glands, Bergh's ptyaline gland, Vayssi re's poison gland, and their coiled, unpaired duct correspond to those of other *Dendrodoris* species (Hoffmann, 1938, p. 919). The salivary glands (*q*) are short sacs. The stomach is thin-walled and distinguishable from the oesophagus (*n*) by the entrances of the liver ducts. The liver (*l*) lies far behind and shows the generically characteristic posterior median cleft. Close behind the pylorus there is a globular caecum (*j*).

The very big white ovotestis (*ho*) is bilobed. It lies in front of and over the liver. The hermaphrodite duct (*he*) dilates to a spirally coiled ampulla (*ae*) that ends with a short spermoviduct. Immediately following its origin the male duct widens and becomes glandular. This prostatic part (*p*) of the vas deferens forms dense coils and runs forward on the right side ; over the ptyaline glands its diameter diminishes suddenly. The narrow outer part of the vas deferens (*e*) passes through a sheath of connective tissue (*m*) that contains black pigment granules. Within this sheath the vas deferens is surrounded by muscles (*mu*). Sheath and muscular tube containing the efferent duct attain the genital vestibulum (*h*). From the latter a penial pouch (*ei*) invaginates. It surrounds the ectal portion of the vas deferens, a 6.5 mm. long and 0.4 mm. thick penial papilla, pentaradial in transverse section (Fig. 153). The cuticular lining of the papilla bears hooks (Fig. 154) in its outer 2.5 mm. long, portion. The spines that lie farther inwards in the introverted papilla have a small base and a long cusp, the ectal ones a strong base and a small cusp. The spines form irregular quincunxes, not distinct longitudinal or transverse rows.

From the genital vestibulum (*h*) a narrow, straight vagina (*v*) runs inwards. It is not cuticularized. Its mantle of connective tissue contains black pigment granules in two of the three dissected slugs. The vagina debouches into the spherical spermatheca (*t*) together with the exit of the long fertilizing duct (*u*). The spermatocyst (*s*) is a little smaller than the spermatheca. The portion of the uterine duct that leads into the female gland mass (*gm*) is thin and short.

After separation from the spermoviduct a short free oviduct (*o*) enters the voluminous female gland mass (*gm*). The conical terminal part of the latter projects into a female atrium. The oviducal opening (*ni*) lies behind the genital papilla. In front of the papilla a broad and folded orifice (*wo*) leads through a fine canal into a white, globular, vestibular gland (*w*). This was conspicuous in the smallest specimen, but could not be found in two bigger ones.

Occurrence : (1) Beach of Jurujuba, Niteroi, outer part of the bay of Rio de Janeiro. One black slug found by Mr. Willy Hein of the Oceanographic Institute of S o Paulo. (2) Canal of S o Sebasti o, under stones in the tidal zone ; 3 large red and red and black animals collected by Dr. George A. Edwards ; and (3) 1 red and black slug, Ilhabela (E. & E. Marcus leg.). (2) and (3) in November 1955.

Discussion of *Dendrodoris atropos*.

The nomenclature of *Dendrodoris* and *Doriopsilla* was discussed by O'Donoghue (1924a, pp. 560-561 ; 1926, pp. 202-203) and Allan (1932, p. 96). In both genera the gills are retractile. Nevertheless they cannot be included in the Dorididae as a subfamily (Thiele, 1931, p. 440). After the introduction (Odhner, 1934, p. 233) of the section Gnathodoridacea for the mandibulate Doridacea, the Bathydorididae with non-retractile gills, and the Doridoxidae without gills, the Dendrodorididae should also form a section, Porostomata Bergh, 1876, probably together with the more distant (Bergh, 1872a, p. 1114 ; Hoffmann 1940, pp. 69-70) Phyllidiidae.

The absence of a radula, and the individual variability of the colour makes classification of the species of *Dendrodoris* highly subjective. The number of gills is taxonomically of little significance. The widespread Indo-West-Pacific *D. nigra*

(Stimpson, 1855, p. 380), good figures of which were published by Alder & Hancock (1864, pl. 31, figs 13-16), Vayssière (1912, pl. 1, fig. 1), Baba (1936, pl. 3, fig. 3), and others, has been described with eight gills. However the number varies from five (Baba, 1949, p. 154) to ten (Bergh, 1889, p. 843). Before we had seen Bergh's description of *D. atropos* we thought that our black slug from Rio perhaps was *D. nigra*, because after all the colour is still the most important systematic character (Vayssière, 1912, p. 78; key of Barnard, 1927, p. 187). The black component especially seems to be constant, while the red was mostly extracted in our specimen tinging the formalin purplish. The black colour and the "soft blister-like pustules" on the back (Allan, 1932, p. 98) of *D. nigra* agree with our slug from Rio. But the concentration of the nervous system is less in *nigra* (Bergh, 1881c, p. 182; 1905a, pl. 7, fig. 8) than in *atropos*. Already Vayssière (1901, p. 46) stressed this peculiarity of *atropos*. The ptyaline gland of *nigra* is distinctly bilobed (Eliot, 1906a, p. 664; for numbers of figures see p. 1008). The inner organs of *nigra*, pharyngeal bulb, prostatic part of efferent duct, mucus gland, vestibular gland, etc., are more pigmented with black than the corresponding parts of *atropos*. We are now convinced that our black slug must be placed together with the red and black slugs and the red one in *atropos*, as Bergh (1879a) supposed but did not decide (p. 51, note 1).

Apart from the concentration of the central nervous system the inner organs do not afford safe taxonomic characters. The more or less concentrated shape of the posterior gland of the oral tube might be functional. The same may be the case with the caecum that is not even mentioned in the descriptions of several species. The proportion of the lengths of the different portions of the female ducts does not agree in our and Bergh's slugs.

As far as we have seen the literature, the semi-serial arrangement of the seminal receptacles as in *D. atropos* is the rule in the Dendrodorididae, since *Dendrodoris nebulosa* (Pease) (Bergh, 1884a, pl. 5, fig. 28), *D. grandiflora* (Rapp) (Pruvot-Fol, 1954, fig. 131, d), *D. languida* Pruvot-Fol (1954, fig. 132, j), a species from the Atlantic coast of Morocco (Pruvot-Fol, 1953, fig. 30, e), *D. temarana* (*ibid.*, fig. 31, c), *D. rubra* (White, 1951, fig. 20), and *Doriopsilla fedalae* Pruvot-Fol (1953, fig. 34) have it. In *Doriopsilla areolata* Bgh. however the disposition is vaginal (Pruvot-Fol, 1954, fig. 134, c). For *Dendrodoris limbata* (Cuv.) one figure gives the semi-serial (Vayssière, 1901, pl. 7, fig. 7) another rather the serial type (Pruvot-Fol, 1954, fig. 130, b). If the vagina opens into the spermatheca immediately beside the exit of the fertilizing duct, it may be difficult to decide whether the arrangement of the seminal receptacles is serial or semi-serial. The vaginal type, of course, is a good specific character, but it seems to be rather rare.

A cuticular lining of the vagina can, if it is thin, only be verified in sections. An armature of hooks in the efferent duct, though a generic character, is known to be absent occasionally even in big specimens (Bergh, 1879a, p. 64). Therefore one can hardly consider the length of the inward extension of the hooks as specific, though in some species (Pruvot-Fol, 1953, fig. 29 on p. 86) their disposition is peculiar. The vestibular gland is in most of Bergh's descriptions considered as oviducal, sometimes it is called vestibulo-vaginal (Bergh, 1884a, p. 126) and sometimes it opens beside the penis (Bergh, 1890a, p. 964). As mentioned in the preceding diagnosis, we found a big vestibular gland in one specimen, none in two other slugs. Bergh (1879a, p. 65) noted a small rudimentary gland on the duct of the mucus gland of *D. atropos*, while that of our specimen is the most anterior of the genital organs with a duct of its own.

***Lomanotus phiops*, sp. nov. (Figs 155-163.)**

The slug was 6 mm. long alive; preserved it is about 4 mm. long and 1.8 mm. high. Through the transparent body the light brown to olivaceous branches of the digestive gland were evident. They attain the rhinophores, the anterior border of the foot and enter the dorsal appendages up to their tips. Whitish dots, probably

cutaneous glands, and more or less symmetrically disposed black specks far below in the connective tissue are further colour marks.

The body is broadest in front, the tail is pointed. The veil is rounded and bears one pointed digitation on either side. The sheath of the right rhinophore has five, that of the left four cusps in the present specimen. The perfoliation of the club consists of about six leaves. The curved notal ridges start from the rhinophoral sheaths and unite the appendages that can be called cerata. Each ridge is bent into eight undulations, four downwards and outwards, four upwards and inwards. The inward outward waves of both sides lie on a level. There are about twenty cerata on either ridge; the inward ones in the middle are the largest. The cerata are pointed cones which contain knobby branches of the digestive gland. The ridges diminish backwards and the notum of the hind end is plain.

The anterior border of the foot is broad, crescent-shaped and smooth, neither grooved nor notched. Its pointed corners are produced and curved backwards. The middle of the sole shows a longitudinal furrow in the preserved slug (Fig. 157). The genital aperture (*g*) is located under the first right inward curve of the ridge, the anus (*a*) in front of the second. The renal pore lies immediately behind the anus, the renopericardial duct (Fig. 163, *r*) farther in front. The middle of the notum bulges where the heart (*h*) lies in a spacious pericardium.

The horny yellow jaws (Fig. 159), the stripes that go out from the hinge, and their scaly masticatory processes agree well with Bergh's detailed description of the mandibles of *L. genei* (1879, pp. 556-557) and Eliot's statements for the same species (1906, p. 350, pl. 11, fig. 8) and *L. marmoratus* (*ibid.*, p. 352). The radula (Fig. 161) consists of about fifteen rows, its formula is about 15, 0, 15. As in the other species of *Lomanotus* the radula can hardly be spread out evenly and counted. The first, innermost teeth are smooth, not denticulate, the following ones have denticles, the number of which increases from five to fifteen or more farther outwards. The number of denticles on either side of the cusp is often different. The base of each tooth is as long as the cusp. The outermost tooth has only few thin and long denticles.

The sections show cyanophilous foot glands (*z*) which are especially dense along the entire anterior border, and two thick tubes of the salivary glands that reach far backwards. The oesophagus is very short. The ample stomach (*s*) is lined with an epithelium bearing dense cilia. Among the flocculent gastric contents evidently originating from Hydrozoa, fragments of Arthropods, perhaps Crustacea, and Diatoms were recognized. The narrow ciliated intestine (*i*) leaves the stomach posteriorly and runs along the right side under the skin. The common root of the liver is localized in the posterior part of the stomach too. This root ramifies immediately so that anterior right (*b*) and left (*c*) diverticula originate. The latter com-

FIGURES 155-163.

Lomanotus phiops, sp. nov. (Figs 155-163.)

FIG. 155.—Sketch of living slug.

FIG. 156.—Preserved slug.

FIG. 157.—Fore end of same.

FIG. 158.—Reconstruction of digestive canal.

FIG. 159.—Jaw plates.

FIG. 160.—Platelets of masticatory process.

FIG. 161.—Teeth of radula, including innermost and outermost.

FIG. 162.—Diagram of reproductive organs.

FIG. 163.—Transverse section on level marked in Fig. 158.

a—anus. *b*—anterior right liver. *c*—anterior left liver. *d*—left branch of posterior liver. *e*—vas deferens. *f*—female gland mass. *g*—genital aperture. *h*—heart. *i*—intestine. *j*—pharynx. *k*—kidney. *l*—right branch of posterior liver. *m*—ampulla. *n*—oviduct. *o*—ovotestis. *p*—penis. *q*—prostatic part of vas deferens. *r*—renopericardial duct. *s*—stomach. *t*—spermatheca. *w*—anastomosis between the branches *d* and *l*. *x*—hermaphrodite ductules. *z*—pedal glands.

municates with the left branch (*d*) of the posterior liver and with a ventromedian tube that also runs backwards. As this tube supplies the posterior right cerata, we call it the right branch (*l*) of the posterior liver. The ventromedian tube unites with the left branch once more (*w*) farther backwards (Fig. 158). Abundant cnidocysts lie within the cells of the central parts of the digestive gland.

The ovotestis (*o*) is of peculiar shape. There are several globular follicles; the centre of each contains sperm. The female cells are produced in numerous smaller acini that surround the spermatogenous sacs. The follicles are united to the ampulla (*m*) by ductules (*x*). At the ectal opening of the ampulla the spermoviduct bifurcates. The male duct begins prostatic (*q*) and then becomes muscular and passes through the penial papilla (*p*), about 0.7 mm. long and 0.35 mm. thick, and especially rich in longitudinal fibres. The penis is melon-shaped, has a terminal though not cuticularized point, and is entirely enclosed in a male vestibulum. This atrium opens at the anterior border of the genital aperture (*g*).

Farther behind open the female organs. In the beginning the oviduct (*n*) is narrow, then it becomes folded and glandular (*f*). A separate vagina does not exist. Only the spherical spermatheca (*t*) is distinguishable entally in the dorsal part of the female gland mass.

Occurrence: 1 slug among algae grown on a boulder in the upper littoral of Ilhabela, island of São Sebastião; 11 November 1955.

Discussion of *Lomanotus phiops*.

Bergh (1892a, p. 1044) distinguished only two species of *Lomanotus*, *L. marmoratus* (Alder & Hancock, 1845) and *L. genei* Verany 1846. Eliot (1906, p. 353) recognized also *L. flavidus* (Alder & Hancock, 1846) that has no raised margin of the back. The same feature characterizes the fourth species, *L. vermiformis* Eliot (1908, p. 88) from the Red Sea. Against Eliot (1910, pp. 162–163) and Odhner (1936, p. 1095) Pruvot-Fol (1954, pp. 364–365) considers *marmoratus* and *flavidus* as juvenile stages of *genei*. Possibly she is right. The farther extension of the liver in *marmoratus* (Odhner, p. 1063) might be a character of young forms as in *Spurilla neapolitana braziliana* MacFarl. Nudibranchs continue to grow after their genital organs are functional (Eliot, 1908, p. 90), and therefore also the diversity of the gonads of *genei* and *marmoratus* (Odhner, p. 1066) can be due to a difference of age. The number of European specimens studied is however small, and hence it seems better, provisionally as Eliot said, to maintain three European species. It is easy to unite them in future, but it is difficult to be sure whether a description associated with the oldest specific name of *Lomanotus* actually refers to a different species.

L. phiops must be compared only with the European species, as *L. vermiformis* is black with specks of white in two dorsolateral bands and has corners of the foot not developed into distinct prolongations. The bases of the radular teeth are shorter than the cusps in the European species of *Lomanotus* with exception of the slug from Naples that Bergh examined (1879, p. 555). This animal and a second from Trieste (*ibid.* 1883a, p. 67) have only one velar process on each side like our specimen, while all other descriptions and figures of the European species indicate four, two on either side. Also the 6 mm. long *L. flavidus* has four tubercular points (Alder & Hancock, 1854, Fam. 3, pl. 41, fig. 7). The number of velar processes of Odhner's key (1936, p. 1095) can no longer be used for separation between the European species and that from the Red Sea, nor does it isolate *phiops*. Disjunctive characters of the latter are the smooth innermost radular teeth and the smooth and entire anterior border of the foot. These teeth bear denticles in the European species, and the foot has a grooved anterior border, the upper lip of which is indented.

The European species were only dissected, and therefore the differences between them and the Brazilian specimen which was sectioned with the microtome cannot be evaluated with certainty. Neither Alder & Hancock's (1848, Fam. 2, pl. 5) nor Odhner's

figures (1936, pp. 1062–1063, figs 1, 2) of the liver, which do not agree with one another, correspond to our Fig. 158. *L. phiops* combines a multiple hermaphrodite gland that encloses the liver on all sides (*genei*; Odhner, p. 1066) with a richly ramified digestive gland (*marmoratus*). The absence of a prostatic part in the male duct (loc. cit., p. 1070) can no longer be considered as a character of the Lomanotidae, since *phiops* has a distinct prostatic part. Moreover it seems that such occurs in European slugs too, as the ental part of the efferent duct of *L. genei* is thickened (Pruvot-Fol, 1954, fig. 142b).

***Hancockia ryrca*, sp. nov. (Figs 164–174.)**

The one living slug was 15 mm. long alive. It glided with its sole adhering to the surface like *H. californica* MacFarl. The inner organs are olive-brown and shine through the vitreous skin that contains white specks, the cnidosacs. The body is fusiform, the tail obtuse and notched. A pair of semilunar prominences (*l*) flanks the mouth and is covered by the bilobate oral velum (*o*). Each lobe of the latter is subdivided into finger-like blunt flaps, seven on the left and nine on the right side. The right side of the body has four, the left, five cerata. These are palmate and end with pointed cusps, eight on the anterior, five on the posterior cerata. The fifth ceras has two, perhaps three points. Branched liver diverticula enter the cerata which also contain many cnidosacs (*c*) on their dorsal and ventral surface.

Hepatic branches and numerous cnidosacs occur also in the funnel-shaped sheaths of the rhinophores (*r*). The sheath forms a cuff with ten tips, each containing a liver diverticulum and many cnidosacs. The club of the rhinophore terminates with a knob that lodges the rhinophoral ganglion and is surrounded by some perfoliations (*ri*) at its base.

The muscular cnidosacs are peculiar organs (Fig. 174) which have only a pore-like communication with the subjacent liver tubule. While in the Eolidacea the cnidocysts generally lie basally in the cells of the cnidosac, and the nuclei apically, positions are inverted here. The sac has no lumen. Possibly the pink-stained mass at the base of the sac that hangs into a space among the liver cells is made up of coalesced cilia of the cnidosac cells. These cilia might lead the nematocysts from the liver lumen to the sac. As in several other cases there are also nematocysts within distal hepatic cells. Here they are apical.

Many epidermal cells are of glandular character (*si*) and include pink secretion or empty vacuoles. Such glandular cells are absent in the velar lobes which have many groups of subepithelial sensory cells (*u*). Clusters of blue mucous glands (*d*) occur on the sole of the foot, especially on its borders. Similarly composed glands (Fig. 168, *ci*) with voluminous, blue staining cells located in the cerata correspond to the branchial glands known from many Doridacea.

The foot is not broader than the body; its anterior end is rounded, its hind end attains the caudal notch.

The pericardial prominence (*ai*) lies between the two first pairs of cerata, and rib-like vessels lead out from it and enter the cerata. The kidney (*k*) is a long tube, brown in the living slug, extending along the entire back and forming transverse branches (*en*) that run out from the central stem with valves (*va*). The nephropore (*ni*) lies on the right side on the level between first and second ceras, immediately dorsal to the anus (*b*).

The central nervous system is like that of *H. californica* MacFarl.

The radula (Fig. 171) has the formula $46 \times 1, 1, 1$. The innermost of the four or five lateral denticles is larger than the median cusp on the rhachidian tooth, and the outer ones decrease in size. The thin lateral teeth have a prominent, cusp-like inner angle. The jaws are extremely delicate. The lateral posterior glands of the oral tube are thick muscular tubes (*h*) with spherical cells around them and extend into the rhinophores. The ventromedian gland (*y*) is a very long, thin sac. Its flat epithelium is granular and is surrounded by a strong musculature and a peritoneum



nearly as high, which becomes lower behind. The salivary glands (*x*) are thin, cyanophilous coils.

The straight oesophagus (*oe*) shows no diverticulum. It enters the stomach (*so*) from the ventral side. The anterior left (*ma*) and right (*me*) liver have a common origin on the left side of the stomach, and the posterior liver also leads out from the left side. The anterior livers supply the rhinophores and the first pair of cerata, all the others receive branches of the posterior liver (*m*). The main trunk of the latter is ventral. The lumen of stomach and liver contained eggs of Crustacea (Fig. 167, *ei*), the former also a Copepod.

Behind the opening of the posterior liver the stomach bends to the dorsal side. Its longitudinal folds bear cuticular ridges in this strongly muscular part (*gi*). The cuticular ridges do not extend to the most anterodorsal, pyloric region of the stomach, from where the intestine (*i*) curves backwards. The anus (*b*) is located at the right side on the level between the first and second ceras.

The ovotestis (*hi*) consists of numerous lobules and lies beneath the kidney and above the posterior liver. Most of the peripheral acini contain female cells and the centre male cells, but this separation is not complete. The ciliated and muscular ductules from the acini unite to the hermaphrodite duct (*he*) which runs forward, then curves back into the ampulla (*a*). The spermoviduct (*s*) leads out from the hind end of the ampulla. A little in front of the anterior end of the latter the spermoviduct bifurcates.

The male branch becomes prostatic (*q*) shortly after its origin, and winds forward and to the right side. There it opens through a short and narrow ejaculatory duct on the dorsal surface of a penial papilla (*p*). Part of the latter is protruded in the present specimen but can evidently project farther or be withdrawn by the felt of crossing muscle fibres of the male atrium. The strong retractor of *H. californica* MacFarl. (1923, pl. 5, fig. 18, pl. 6, fig. 22) is not developed in our specimen, but for the rest the hermaphrodite and male organs of the Californian species agree well with those of the present one.

The female organs are different, as two ducts open into the female atrium (*j*), a vagina (*v*) and a nidamental duct (*n*). The first, a short, curved and muscular tube,

FIGURES 164-173.

Hancockia ryrca, sp. nov. (Figs 164-173.)

FIG. 164.—Dorsal view of living slug.

FIG. 165.—First right ceras of preserved slug.

FIG. 166.—Rhinophore of same.

FIG. 167.—Combined section of rhinophore.

FIG. 168.—Section of "branchial" gland from ceras.

FIG. 169.—Diagram of digestive tract, reconstructed from transverse sections; pharynx was taken out for radula.

FIG. 170.—Combined transverse section of second ceras and body on level of root of anterior liver.

FIG. 171.—Radular teeth.

FIG. 172.—Diagram of male vas deferens.

FIG. 173.—Diagram of female organs.

a—ampulla. *ai*—heart. *b*—anus. *bi*—blood lacunae. *c*—cnidosac. *ci*—"branchial" gland. *cn*—cnidocyst. *d*—pedal glands. *e*—vas deferens. *ei*—crustacean egg. *en*—transverse branch of kidney. *f*—rhinophoral nerve with ganglion. *g*—female gland mass. *gi*—gizzard. *h*—lateral posterior glands of oral tube. *he*—hermaphrodite duct. *hi*—hermaphrodite gland. *i*—intestine. *j*—female atrium. *k*—kidney. *l*—lip. *m*—posterior liver. *ma*—left anterior liver. *me*—right anterior liver. *n*—nidamental duct. *ni*—nephropore. *o*—oral velum. *oe*—oesophagus. *ov*—oviduct. *p*—penis. *q*—prostate. *r*—rhinophore. *ri*—perfoliation. *s*—spermoviduct. *si*—skin gland. *so*—stomach. *t*—spermatheca. *u*—sensory cells. *v*—vagina. *va*—valve of lateral branch of kidney. *w*—fertilization chamber. *x*—salivary gland. *y*—median gland of oral tube. *z*—renopericardial duct.

leads to a voluminous, spherical spermatheca (*t*) with muscular wall. The spermathecal epithelium forms narrow villi of different length, between which the strands of spermatozoa are lodged.

The female branch of the spermovi duct begins with a short oviduct (*ov*) that dilates to a fertilization chamber (*w*) and then runs into the gland mass (*g*). The duct from this (*n*) opens through several folded outlets into the muscular female atrium (*j*). The latter lies behind the male atrium, completely separated from it. The aperture of the spermathecal canal or vagina lies opposite to one of the nidamental orifices so that the sperm can pass from the spermatheca to the fertilization chamber. The genital openings are situated on the right side, on the level between rhinophore and first ceras.

Occurrence: Coast of S. Paulo, 14 km. west of Ubatuba, 1 specimen among *Padina* near the low-water line; September 1955.

Discussion of *Hancockia ryrca*.

MacFarland (1923, p. 65) introduced a special family Hancockiidae for the present genus, and Odhner (1936) included this family in his suborder Dendronotacea (1934, pp. 230-231, 285).

The genus *Hancockia* Gosse, 1877 contains three species, one from the South English, French Atlantic, and Mediterranean coasts (Cuénot, 1927, p. 265), *H. uncinata* (Hesse, 1873), *H. californica* MacFarland, 1923, and the Indic *H. papillata* (O'Donoghue, 1932). Trinchese's Mediterranean species were united with the Atlantic one by Eliot (1906, p. 354) and Pruvot-Fol (1931, p. 753; 1951, p. 51; 1954, p. 360). Only the last author calls the European species *H. uncinata* (Hesse, 1873); all others, including Cuénot, apply the name *eudactylota* Gosse, 1877. In the descriptions and figures of Hesse (1873), Gosse (1877), Gamble (1892) and Eliot (1906; 1912) the number of appendages of the velar lobes varies from 3 to 9, and that of the tips of the cerata from 3 to 14. There are no differences that justify specific separation, so that the name must be *uncinata* (Hesse).

The radula of *H. californica* differs from that of the present species by having equal lateral denticles on the rhachidian tooth. The female reproductive organs of *californica* do not agree with those of *ryrca*. MacFarland mentioned a spermatheca and a fertilization chamber, but his figures (pl. 5, fig. 18, pl. 6, fig. 22) do not actually show any vagina. Also the shape of the cerata in *californica* is quite different, and the anterior liver lobes are completely separated.

We know *H. papillata* (O'Don.) only from Thiele (1935, p. 1004) and Odhner (1936, p. 1104). The latter included it in the genus *Hancockia* and separated it from the European and the Californian species. It is improbable that a 4 mm. long slug like *papillata* with seven pairs of cerata each with eight or nine knobs is conspecific with the present animal which has fewer cerata with fewer points, though it is very much longer.

It is not easy to compare *H. ryrca* with *H. uncinata* (Hesse) because the latter is not sufficiently described. All the 18 figures of *Hancockia* in Bronn refer to *californica*. Eliot's figure of the radula (1906, pl. 11, fig. 10) shows lateral teeth which differ considerably from those of *ryrca*, but his text (p. 355) is compatible with our radula. The rhachidian tooth of *uncinata* has lateral denticles all of equal size with the median cusp (Odhner, 1936, p. 1105), not the large paramedian denticles of *ryrca* and its smaller outer ones. Another distinguishing character is the separate origin of the anterior liver tubes in *uncinata* (Eliot, 1906, pl. 11, fig. 11). The absence of the oesophageal diverticulum that occurs in *uncinata* and *californica* could not be verified in *ryrca* with the certainty required for negative characters. The reproductive organs of *H. uncinata* are well known (Odhner, 1936, p. 1068, fig. 9). They agree with those of *ryrca*. A fertilization chamber is not described for *uncinata*, but possibly this organ is not separated from the fertilizing duct when it is empty.

Doto pita Marcus. (Figs 175–179.)

Living slugs from *Padina* in the littoral of Ilhabela were up to 7 mm. in length. They were vitreous when alive, with brown spots on the back and white tips to the cerata, which stand in four or five pairs. The generative organs of three mature animals were studied in serial sections.

The hermaphrodite gland (*r*) consists mainly of mixed follicles, in which the development of male cells precedes that of the female ones. Follicles that contain only male or female germ cells occur, but evidently these represent an early or late stage of the mixed follicles. A more peripheral or central position of follicles with only male or female cells was not observed.

The hermaphrodite duct (*h*) enters a spherical ampulla (*a*), and close to its entrance the spermoviduct (*u*) leaves the ampulla. The separation of efferent duct (*e*) and oviduct (*o*) takes place at some distance from the ampulla.

The ciliated male duct (*e*) opens into the prostate (*q*) which begins as a simple ciliated dilatation of the duct. Later on it develops into a voluminous glandular pouch that extends entirely beyond the entrance of the efferent duct. Then its total length is 0.25 mm., its diameter 0.15 mm. The aspect of the secretory prostatic epithelium suggests the activity of the nuclei in producing the secretion known in so many glands. In the beginning the nuclei lie near the free surface of the cells with only a narrow cap of secretion over them. Later on the cones of secretion increase, the cilia disappear, and the nuclei are located farther from the surface. Finally nearly all cytoplasm is transformed into secretion, and the nuclei lie near the bases of the cells. From the prostate the efferent duct continues winding ectally for about 0.4 mm. into the penial papilla (*p*). The length of this papilla is 80 micra. It projects with a more or less distinct point into the male atrium (*m*) which opens on the genital papilla, dorsally to the female openings.

The long winding oviduct (*o*) has several communications with the female gland mass (*g*) and opens through several outlets or nidamental ducts (*w*). From the most dorsal of these a ciliated vagina (*v*) goes inwards. It has a thin sphincter in the middle and a stronger one at the entrance of the spermatheca (*s*). This capacious vesicle lies between ampulla (*a*) and prostate (*q*). All spermatozoa in the spermatheca are directed with their heads to the ventral side. The youngest slug has an enormous spermatheca and a small ampulla, probably because the former was filled and the latter emptied in the first mutual exchange of sperm. In the older slug spermatheca and ampulla are of equal size. In the oldest sectioned specimen, nearly without sperm in the ovotestis, the ampulla is swollen and the spermatheca small. Accordingly mature slugs produce, at least, 2 sets of eggs and larvae.

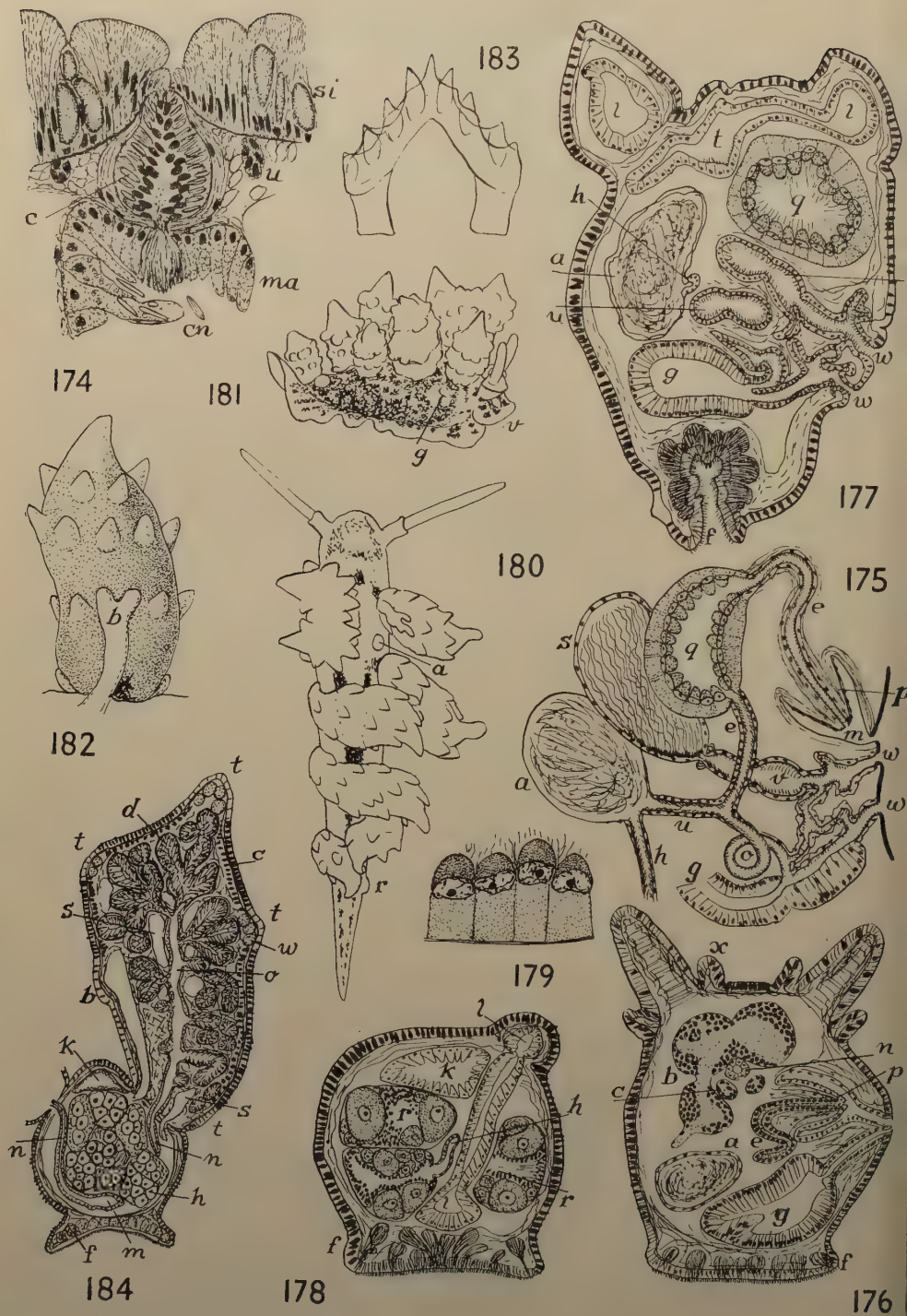
The spawn of *D. pita* found on Sertulariids is a wavy tube, not unlike Pruvot-Fol's figure 157, *c* (1954).

Our description differs in several details from Odhner's (1922, pp. 39–41). The follicles of the hermaphrodite gland of *Doto coronata* (Gmel.) and *D. antarctica* Eliot (Odhner, 1934, p. 303) are male and female separated, and the ampulla is sausage-shaped. These differences may be specific. The same may hold good for the shortness of the oviduct in *D. coronata*. The male vesicula seminis of *D. coronata* does not occur in *D. pita*, and its prostate does not have such a long winding caecum as in *D. coronata*.

As *Doto pita* has a male tube, "a channel for fertilization, and a channel for oviposition" (Eliot, 1910, pp. 58–59), it must be considered as triaulic, though Odhner (1936, p. 1070) called the Dotonidae diallic.

Doto uva Marcus. (Figs 185–186.)

We have now found two slugs, about 8 or 9 mm. alive, one with seven, the other with eight pairs of cerata. Therefore *D. uva* comes to another group of Odhner's key (1936, pp. 1119–1121), namely I A. One of the living slugs was light pink, the other



light yellow. After fixation in "Susa" the specimens became nearly black in alcohol. Therefore we compared them once more with *D. obscura* Eliot (1906b, p. 152) from the Cape Verde Islands. The boss (*b*) in front of each rhinophore that Eliot described occurs also in our slugs, but this character is not specific (Odhner, 1934, p. 301). Several differences make a union of *uva* and *obscura* impossible. *D. obscura* is a strongly pigmented species, the living animals of which are red-brown when young and black or grey mottled when adult. The veil is round, while that of *uva* is expanded and angled. In our first description (Marcus, 1955) we called the velum of *D. uva* "slightly expanded", but it is distinctly produced (Fig. 185, *t*). Eliot called the anterior process of the rhinophorial sheath a "lip", we a "beak", an indication that these formations are longer in *uva*. The radula of *obscura* consists of 72 teeth (length of slug 7 mm.), that of *uva* contains 86 (length of living animal 4.5 mm.).

Like our first specimen (Marcus, 1955, pl. 24, fig. 221) the new material shows very big crystals in the renal lumen and cnidocysts in the cavity of the digestive gland.

The reproductive organs agree with those of *Doto pita* in essentials, but differ considerably in details. The follicles of the ovotestis are mixed, containing male as well as female cells. The ampulla (*a*) is sausage-shaped as in the species mentioned in the preceding description which Odhner examined (1922; 1934). The spermoviduct (*u*) is very short, and the male duct becomes prostatic (*q*) immediately ectal to its origin. The muscular outer portion of the male duct, an unarmed conical penis (*p*), is very long and included in a fusiform atrial sac (*m*) as was described for *Doto antarctica* Eliot (Odhner, 1934, p. 303).

The oviduct is short and chamber-like, thus very different from that of *D. pita*. The outlet (*w*) of the female gland mass (*g*) is simple; the nidamental duct receives a long and wide ciliated uterine duct (*d*) from the rather distant vagina (*v*). The latter leaves the atrium and leads to a voluminous spermatheca (*s*) the entrance of which is provided with a well developed sphincter.

Occurrence: Upper littoral of Ilhabela among algae with Sertulariids.

FIGURES 174-184.

Hancockia ryrca, sp. nov. (Fig. 174.)

FIG. 174.—Section of cnidosac. For lettering see Figs 164-173.

Doto pita Marc. (Figs 175-179.)

FIG. 175.—Diagram of reproductive organs.

FIG. 176.—Transverse section on level of male aperture.

FIG. 177.—Same on level of female openings.

FIG. 178.—Same on level of ovotestis.

FIG. 179.—Cells of prostate.

The sections are taken from different slugs.

a—ampulla. *b*—central nervous system. *c*—buccal ganglia. *e*—vas deferens. *f*—foot with glands. *g*—female gland mass. *h*—hermaphrodite duct. *k*—kidney. *l*—liver. *m*—male atrium. *n*—oesophagus. *o*—oviduct. *p*—penial papilla. *q*—prostate. *r*—hermaphrodite gland. *s*—spermatheca. *t*—stomach. *u*—spermoviduct. *v*—vagina. *w*—nidamental apertures. *x*—rhinophoral sheath.

Doto caramella, sp. nov. (Figs 180-184.)

FIG. 180.—Sketch of living slug.

FIG. 181.—Preserved slug, right side view.

FIG. 182.—Second right ceras seen from mid-line.

FIG. 183.—Radular tooth.

FIG. 184.—Transverse section on level of second ceras.

a—anus. *b*—gill. *c*—skin glands. *d*—lobules of digestive glands. *f*—pedal glands. *g*—genital apertures. *h*—ovotestis. *k*—kidney. *m*—main stem of digestive gland. *n*—diverticulum of same to ceras. *o*—liver duct in ceras. *r*—regenerating ceras. *s*—blood sinus. *t*—tip of ceras and tubercles. *v*—velum. *w*—"defensive" glands.

***Doto caramella*, sp. nov. (Figs 180–184.)**

The slug was 8 mm. long alive and about 3.5 mm. preserved, with body 1 mm. high and cerata 2 mm. long. The rhinophores are smooth and colourless, 2 mm. long in life. Whitish dots on the rhinophores are cutaneous glands. In the preserved state the rhinophore sheaths have slightly wavy margins. The veil is evenly rounded; in the preserved slug it is a little set off (*v*) from the head at the sides.

The body is transparent with star-shaped melanophores on the back of the head and on the trunk as well as at the bases of the cerata. The cerata themselves are nearly free from black pigment. They are coloured opaque orange and tipped with white. Also the pointed tubercles are white. These are rather distant from one another and form four rings around the ceras. The orange colour is contained in the hepatic lobules (*d*) and the skin glands (*c*) which are absent in the tubercles and in the tip of the cerata (*t*).

The present slug has four right cerata the last of which is regenerating (Fig. 180, *r*). There are five cerata on the left side, the first two of which are fused and contain two hepatic diverticula. Such coalescence of cerata is rare (Hoffmann, 1934, p. 358). The inner side of the cerata bears a gill (*b*) which is distinct though little branched.

The section (Fig. 184) shows that the gill is characterized by a gland-free epidermis and an underlying blood sinus (*s*). This sinus continues branching upwards in the ceras and communicates with a sinus of the outer side of the ceras. Both sinuses have sphincters at the root of the ceras. The latter with the diverticulum (*n*) of the digestive gland between inner and outer sinus corresponds to Trinchese's figure (Hoffmann, 1940, fig. 55B) of the Saccoglossan *Ercolania siottii* Trinchese (1872, p. 121). The liver duct (*o*) in the ceras is richly lobed (*d*). The epithelium of the duct is flat, that of the lobules so high that it fills the lumen. The cutaneous glands (*c*) are cyanophilous in the sections; the subepidermal, so-called defensive glands (*w*) localized in the tip and the tubercles (*t*) of the ceras stain pink.

The jaws are delicate. The radula has 91 (or perhaps more) teeth which are as high as broad and have three denticles on either side of the slender median cusp (Fig. 183). The anus (*a*) lies to the right of the mid-line between first and second ceras. There are no crystals in the kidney (*k*).

The reproductive organs, the analysis of which is difficult in *Doto*, could be recognized only in part. The large follicles of the ovotestis (*h*) are mixed, containing male and female elements. The prostate is a very long, coiled part of the efferent duct. The muscular penis is short, only a little longer than thick and enclosed in an atrial sac. The genital apertures (*g*) lie ventrally to the first right ceras.

Occurrence : Island of São Sebastião, 1 slug on Sertulariids attached to algae in the upper littoral of Ilhabela; November 1955.

Discussion of *Doto caramella*.

A species with white-topped tubercles of the cerata as in Odhner's group II and with pointed tubercles as in group III does not fit into the key (1936, pp. 1119–1121). As the orange colour of *caramella* fades in alcohol and may be supposed to disappear completely when the material is preserved for years, we think that chiefly group III must be considered.

As the criterion "a distinct gill" or "no distinct gill" is difficult to verify in some of the older species, we must compare *D. caramella* with the five species of group III which have four to six pairs of cerata. *Doto kabretiana* (O'Donoghue, 1929) has a projecting anterior lip of the rhinophoral sheath and a perfoliate club (p. 831), perhaps similar to the annulate one of *Doto crassicornis* M. Sars, 1870 ("tentaculis transverse sulcatis"). *Doto apiculata* Odhner, 1936 (= *Doto spec.* Bergh, 1904, p. 13) has much more prominent tubercles on the cerata than *caramella*, its tubercles stand in six to seven rings, and the frontal veil is produced laterally. *D. cuspidata* Alder & Hancock,

1862 (Eliot, 1910, p. 123) differs from our species by scalloped margins of the rhinophore sheaths and by the veil produced into recurved points at the sides. The body is white or yellow, spotted with pink or purple. Also the colour of *D. cornaliae* Trinchese, 1882, which has no black elements, differs widely from that of *caramella*, and its veil is broad and bilobed. *Doto aurea* Trinchese, 1882, is a somewhat doubtful species (Pruvot-Fol, 1954, pp. 406, 407) with deeply lobed rhinophore sheaths and prominent though slightly pointed tubercles of the cerata.

Among the group of *Doto* with apical spots of the papillar tubercles paler than general colour (Odhner's group II) *D. cinerea* Trinchese, 1882 must be compared with *caramella*. The original figures of *cinerea* (pl. 55) are similar with regard to the shape of the body, the veil and the cerata. But the tubercles of the cerata of *cinerea* (loc. cit., fig. 2: Pruvot-Fol, 1954, p. 406) are distinctly rounded so that *caramella* cannot be this species.

***Catriona tina*, sp. nov. (Figs 187–198.)**

The slender slugs are up to 3 mm. long alive and have a long, pointed tail (1 mm.). Preserved, their maximum length is 2.1 mm. One of the sectioned slugs (preserved 1.6 mm.) was 0.36 mm. high and about 0.3 mm. broad. The tentacles (*t*) are 0.3 mm., the rhinophores (*r*) 0.6 mm. long. The longest cerata are 0.5 mm. in living and preserved animals; they are club-shaped and bear cnidosacs 0.15 mm. long set off from the clubs. Nematocysts occur also in the hepatic cells.

The fore end of the foot (*f*) is a little broader than the following part; the head is not broader than the body. The anterior border of the foot is slightly concave, its corners are rounded.

The animals are whitish with brown hepatic tissue. Subepidermal dots which are white in reflected, brown in transmitted light, occur on head, rhinophores, and back. There is an orange ring near the base on the rhinophores, and small spots of the same colour between the eyes and the first cerata (Fig. 187).

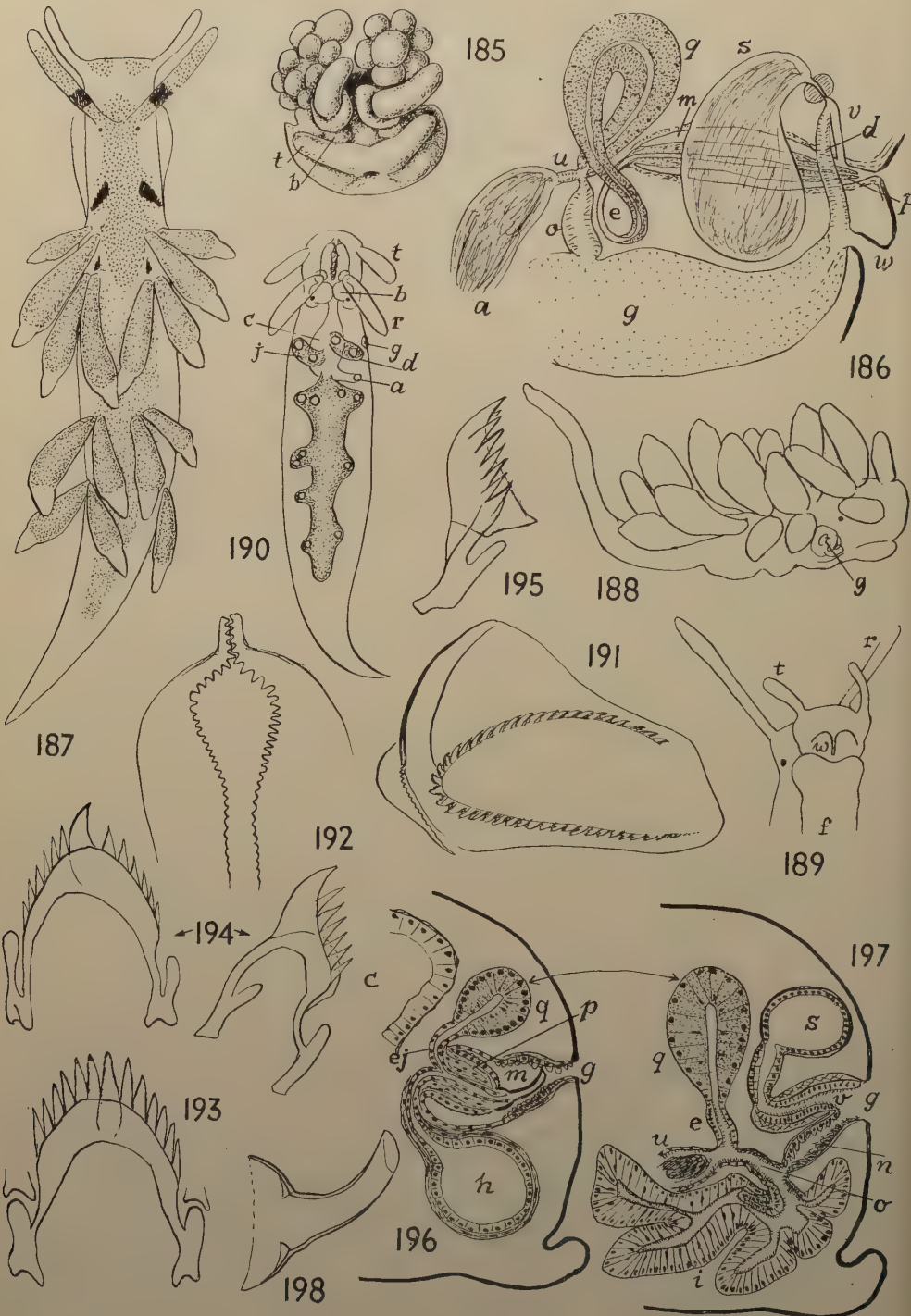
The cerata form four or five groups on each side, the first two of which are nearer to one another than the second and third. The groups do not always occupy the same level on both sides. More than eight cerata on one side were not seen. The first groups contain two cerata each, the following ones, one or two. The right liver (*d*) forms only one duct, as does the anterior left liver (*j*).

The anus (*a*) lies between the right liver and the foremost right branch of the left liver, 0.82 mm. from the anterior end. The gonopore (*g*) is located in front of the first group of cerata, 0.45 mm. behind the tip of the head. The male atrium (*m*) opens into the common atrium, 40 micra in front of the vaginal and nidamental pores. The outer genital opening is undivided (Figs 196–197, *g*).

The mandibles are 0.25 to 0.3 mm. long, and thin, except the strengthened yellowish anterior border. The masticatory process (Fig. 192) bears about 30 fine pointed teeth. The radula has 49 teeth. The minute first teeth are preserved, and the upper and under limb of the radula nearly meet behind. The teeth (Figs 193–194) are horseshoe-shaped and have very deep hinge grooves. The median cusp is a little stronger than the six denticles of each side and elevated on a crest so that it rises farther back than the denticles.

Long glands of the anterior alimentary tract, the openings of which were not seen, are probably salivary glands, not posterior glands of the oral tube (Bergh, 1883*a*, pp. 56, 59; Hoffmann, 1938, p. 924), because they pass through the nerve ring (*ibid.*, p. 907). Their thin branching tubes extend far backwards, ending about 0.9 mm. from the tip. Series of spherical glandular cells are mingled between the low epithelium of the central tube.

The heart is distinct in living slugs and in the sections; the pericardium extends from 0.7 to 0.79 mm. behind the anterior end, the kidney from 0.65 to 1.05 mm. The renal pore lies shortly before the anus.



The male and female follicles of the hermaphrodite gland are separate and approximately spherical. There were three and four male, and six and eleven female follicles in two sectioned slugs. Ectally to the ampulla (*u*) a short ciliated vas deferens (*e*) follows. It continues with a much longer (90 micra) prostatic (*q*) course (60 micra in diameter), that leads to the penial papilla (*p*). Here the ejaculatory duct (*ej*) receives the efferent canal of a voluminous (diameter 0.12 mm.) muscular penial gland (*h*). The papilla is 80 micra long, 50 micra thick and bears a curved, obliquely truncated tubular stylet, 40 micra long and 10 micra broad at its base (Fig. 198).

The female branch which leaves the hermaphrodite ampulla, the oviduct (*o*), enters the female gland mass (*i*), through the lobes of which it continues as a ciliated furrow. The outer part of the oviduct, the nidamental duct (*n*), is set off from the gland mass as a distinct canal. Dorsally to it the wide vagina (*v*) with its strong annular muscles runs inward. The vagina forms a sharp angle with the canal of the spermatheca that comes from the dorsal side. The spermatheca (*s*) is 90 micra long and 60 micra broad and high.

Occurrence: Island of São Sebastião and 14 km. west of Ubatuba, June 1953 and July 1955. Four specimens among *Padina* in the upper littoral.

Discussion of *Catriona tina*.

Winckworth's diagnosis of the genus (see Odhner, 1944, p. 22) does not exclude a species with only one row of cerata belonging to the right lobe of the liver. As a rule, it is true, there are at least three (Odhner, 1939, p. 53). Species of *Cratena* (sensu Bergh) with two right pre-anal rows of cerata are *Cratena bylgia* Bergh (1870, p. 5, pl. 3, fig. 16) and *C. cucullata* Bergh (1905, p. 230). Their generic position cannot be settled, as long as only the broad (*Cuthona*) or narrow head (*Catriona*) and the more (*Cuthona*) or less (*Catriona*) prominent cusp of the radular tooth is considered. The diagnosis of *Catriona* should include the armature of the penis. If the radular tooth is not examined in an exact surface view (Fig. 193), but only a little slanting (Fig. 194), even the cusp of a *Catriona* may project. The common wall of the male and female genital opening (*Catriona*) and their external separation in *Cuthona* (Odhner, 1926, p. 27) are further

FIGURES 185-198.

Doto uva Marc. (Figs 185-186.)

Fig. 185.—Frontal view of preserved slug.

Fig. 186.—Diagram of reproductive organs.

a—ampulla, *b*—prerhinophoral boss, *d*—fertilising duct, *e*—vas deferens, *g*—female gland mass, *m*—atrium, *o*—oviduct, *p*—penis, *q*—prostate, *s*—spermatheca, *t*—expansion of veil, *u*—spermoviduct, *v*—vagina, *w*—oviducal aperture.

Catriona tina, sp. nov. (Figs 187-198.)

Fig. 187.—Dorsal view of living slug; the orange spots are drawn in black.

Fig. 188.—Lateral view of preserved slug.

Fig. 189.—Ventral view of fore end of other specimen.

Fig. 190.—Alimentary canal.

Fig. 191.—Jaws and radula seen from the left side.

Fig. 192.—Masticatory processes seen from below.

Fig. 193.—Surface view of radular tooth.

Fig. 194.—Two slanting views of same.

Fig. 195.—Side view of same.

Fig. 196.—Combined transverse section of male organs.

Fig. 197.—Same of female organs, about 40 micra behind the former.

Fig. 198.—Stylet of penis.

a—anus, *b*—central nervous system, *c*—stomach, *d*—right liver, *e*—vas deferens, *ei*—ejaculatory duct, *f*—foot, *g*—genital aperture, *h*—penial gland, *i*—female gland mass, *j*—anterior left liver, *m*—male atrium, *n*—nidamental duct, *o*—oviduct, *p*—penial papilla, *q*—prostatic part of vas deferens, *r*—rhinophore, *s*—spermatheca, *t*—tentacle, *u*—ampulla, *v*—vagina, *w*—lower lips.

distinguishing characters. *Piseinotecus divae* Marcus, 1955, has a broad head, separate male and female pores, and its radula resembles that of *Cuthonella* (now *Cuthona*) *paradoxa* Eliot (1907a, p. 24). However it differs from *Cuthona* by its single pre-anal liver duct and prominent foot corners. Moreover it has not the long tongue of *Cuthona* (and *Catriona*), the whole underside of which bears teeth (Odhner, 1939, p. 69).

The "*Cratena*-species" from the Western Atlantic listed and in part described by Bergh (1886, pp. 28-32) need not be discussed, because they have more numerous rows of cerata than *tina*.

Very similar to our species is a specimen from the coast of Morocco (Pruvot-Fol, 1953, pl. 2, fig. 24). It is said to resemble *Eolis amoena* Alder & Hancock (1845, Fam. 3, pl. 30), and also *Eolis olivacea* Ald. & Hanc. (1845, Fam. 3, pl. 26), which according to Alder & Hancock (1855, p. X) is identical with *Eolis foliata* (Forb. & Goods.). *E. amoena* is a generically not yet settled Cuthonid (Eliot, 1906, p. 368); after Pruvot-Fol (1954, p. 384) probably it belongs to *Catriona*. It cannot be our species, because it has a short radula (Alder & Hancock, 1855, explanation of pl. 47, Suppl.). *E. foliata* certainly belongs to *Catriona* (Eliot, loc. cit.) or *Trinchesia*, as Pruvot-Fol (1954, p. 381) writes, and is very similar to *C. tina*. *C. foliata* is evidently a somewhat variable species; the British specimens are short-tailed, while Løyning's from Norway (1922, pl. 3, fig. 12) have, like *tina*, "eit langt, smalt haleparti". The mandibles of these slugs "er lange og smale", unlike those of *tina*, but Odhner (1939, p. 75) described and figured a "comparatively short jaw". The hinge grooves of the radular teeth of *foliata* (*olivacea*) are less profound than in *tina*, as is shown by Alder & Hancock's (1855, pl. 47, Suppl., fig. 20), Eliot's (1906, pl. 11, fig. 16), and Løyning's (1922, fig. 42) figures. Moreover we have not seen *tina* with a right liver consisting of more than one duct with two cerata, so that it cannot well be united with *foliata* which has four pre-anal rows together with about ten cerata (Odhner, 1939, fig. 42).

***Tergipes despectus* (Johnston). (Figs 199-204.)**

Eolis despecta Alder & Hancock, 1845, Fam. 3, pl. 36; 1846, Fam. 3, pl. 8, fig. 8; 1855, p. 52 (*Tergipes*) pl. 47, Suppl., fig. 28, App. p. XII, XXIII (*Tergipes*).

Tergipes despectus Bergh, 1879, p. 571, pl. 8, figs. 11-16.

Eolis despecta Hecht, 1895, p. 549 (*Tergipes*) pl. 1, fig. 4.

Tergipes despectus Eliot, 1910, p. 170.

Tergipes despectus Pruvot-Fol, 1951, p. 62, pl. 4, fig. 12 (a very young specimen).

Tergipes despectus Pruvot-Fol, 1954, p. 378, fig. 148.

The single specimen was 2.5 mm. long alive. The height of the transverse sections is 0.4 mm., the breadth 0.3 mm., half of which is occupied by the sole. The slug is white with scattered little spots of brownish-grey colour. The liver is brown. The anterior border of the foot is rounded. The tentacles are 0.1 mm., the rhinophores 0.3 mm., and the cerata up to 0.4 mm. long, measured in the sections. The first pair of cerata lies on the same level, while the second to fourth left cerata are anterior to the corresponding right. The second and third left cerata of the present specimen are in regeneration and therefore small. The complete cerata are claviform, and their greatest breadth lies in the upper half.

The anus (*a*) is situated in the interhepatic space a little in front of the middle of the slug and to the right of the mid-line. The renal pore (*n*) lies close behind the anal opening, the common genital aperture beside and slightly behind the right rhinophore.

The mandibles were not obtained in the only available specimen; according to Bergh (1879, p. 572) the short masticatory process has a single row of blunt denticles. The radular teeth agree better with Alder & Hancock's figure (1855, loc. cit.) than with Bergh's (1879, pl. 8, fig. 14), since the median cusp is about twice as long and thick as the seven to nine lateral denticles, not thrice as long as in Bergh's drawing. Oesophagus, stomach, and intestine are lined with high epithelium that is densely

ciliated. The oesophagus enters the dilated stomach from the anterior side. Farther behind the left anterior liver duct (*v*) leaves the stomach. The right hepatic canal (*u*) leaves at the level of the pylorus, and the left posterior liver branch (*w*) from the hind end of the stomach. The space between skin and hepatic diverticula in the cerata is filled with connective tissue which contains numerous "special cells" (Hecht, 1895, p. 661). These probably act as reservoirs of food (Evans, 1922, p. 453, after Henneguy 1925, p. 424) in liquid form. Hoffmann (1935, pp. 534-535) unites these storing "special" cells with the vesicular cells of Leydig. The short, pore-like communication between the hepatic tubule and the cnidosac (Hecht, 1895, p. 582) was drawn by Herdman & Clubb (1892, pl. 33, fig. 19). The wall of the cnidosac is strongly muscular.

The kidney (*k*) is a simple dorsomedian tube which is 0.7 mm. long and ends 0.4 mm. before the tip of the tail. The renal cells fill up the greatest part of the organ, the lumen of which is restricted to the vicinity of the renopericardial canal (*r*) and the nephroproct (*n*). Some cells contain eosinophilous granules and others vacuoles. Small dark staining masses surrounded by cytoplasm were seen in the lumen (Fig. 202) suggesting merocrine excretion.

The follicles of the hermaphrodite gland are male (*t*) and female (*o*) in the present specimen: Herdman & Clubb (1892, p. 551) occasionally observed mixed ones. The spermiduct (*s*) enters the spacious ampulla (*b*) from the dorsal side. The male and female ducts leave the ampulla separately. The efferent duct begins wide and with a low epithelium. Farther on, it narrows, and its epithelium becomes high and ciliated (*e*). Then it enters the muscular penis (*p*), 0.14 mm. long and 80 micra thick. The penis of the present slug is partially protruded from the male atrium (*d*). The tip of the stout penial papilla bears a cuticular spout, about 20 micra in diameter, the exact shape of which could not be determined from the sections. As in other Cuthonidae (Odhner, 1939, pp. 67-68) a penial gland (*m*) opens into the efferent duct shortly before the opening of the latter. This gland is 0.25 mm. long and 0.1 mm. thick. Its high cells are stuffed with eosinophil granules; its wall is muscular. As the efferent duct has no glandular portion, the penis gland evidently functions as "prostate". Other Cuthonidae, it is true, have a penial gland besides a prostatic portion of the efferent duct.

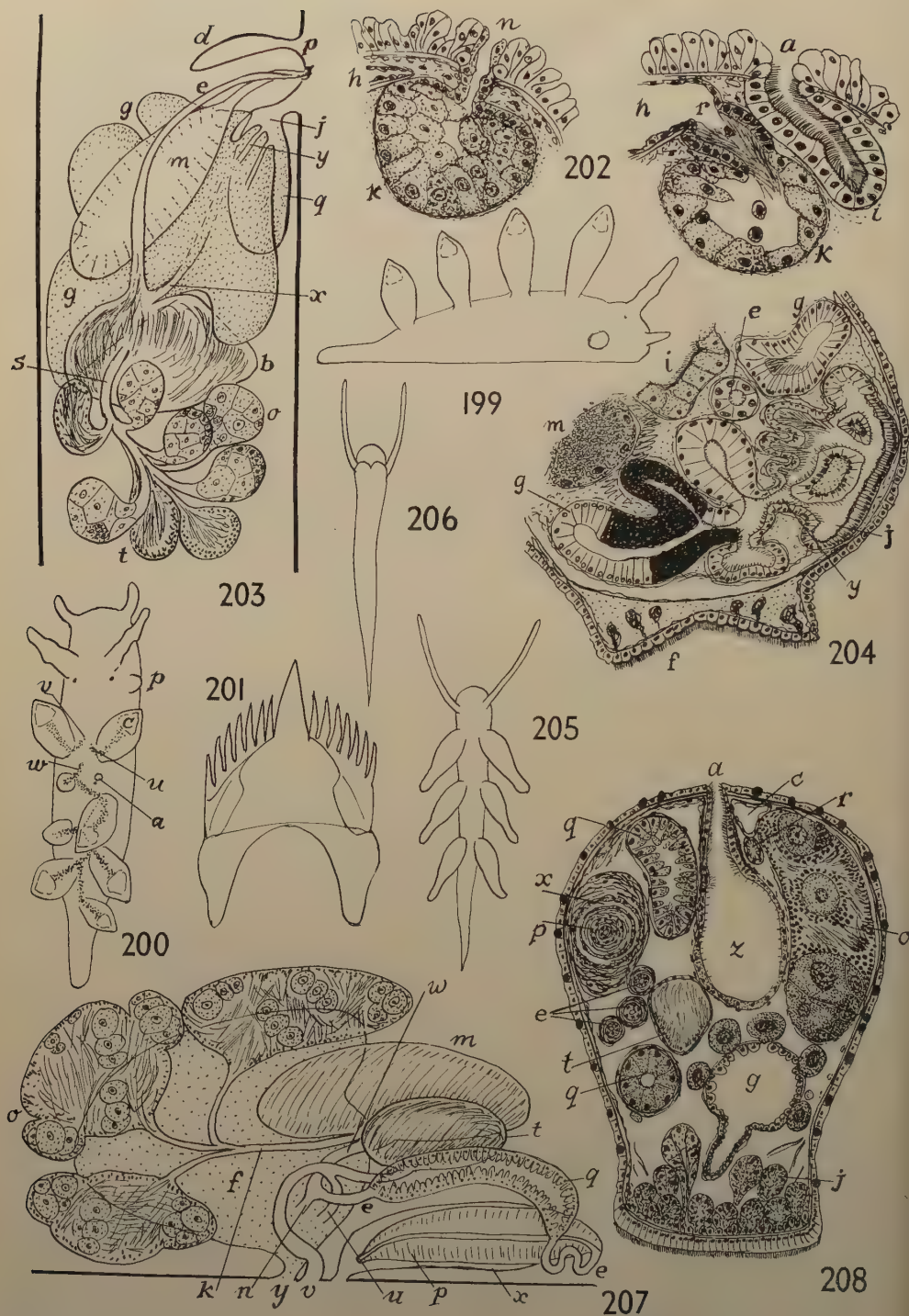
The oviduct (*x*) enters the "female gland mass" (*g*) as it is called by common consent, although it is actually the functional oviduct, the loops of which have different histological characters. It resembles *Calma glaucoidea* (A. & H.), in which the dorsal wall is coiled and ciliated, forming, after Evans (1922, p. 451) a twisted egg-passage, while the ventral wall is flat and thin, leading incoming sperms. The outlet of the gland mass into the female atrium (*j*), the nidamental duct, is multiple (*y*). The spermatheca (*q*) is a pouch, 0.11 mm. deep and just as broad, of the posterior wall of the female atrium. Apart from its distally broad communication with the atrium the spermatheca of the present species agrees with the receptaculum seminis of *Calma glaucoidea* (Evans, 1922, text-fig. 2, *r.s.*).

Occurrence: Bay of Santos, Ilha Porchat. One mature specimen collected by the staff of the Oceanographic Institute, 13 September 1954.

Notes on the distribution of *Tergipes despectus*.

Tergipes despectus (Johnst.) is a European boreal species which occurs on the coasts of Great Britain, Brittany (Cornet & Marche-Marchad, 1952, p. 38: on *Obelia*, after Teissier), Belgium, Netherlands, and Germany, northward to the coasts of the Skagerrak, Southern Norway (Bergen), Faroes and Iceland. The references mentioned in the synonymy, as well as Engel (1936), Hoffmann (1926), Jaekel (1952), Lemche (1929, 1938, 1941), L  yning (1927), and Odhner (1939, p. 76) contain the data on the European distribution.

The North American localities, Boston and Gloucester, Mass., for *Aeolis despecta* (Gould, 1870, p. 248, pl. 16, figs 222-225) refer to a species with 4 to 7 pairs of cerata.



Johnson (1934, p. 155) records a species that he calls *Tergipes despectus* (Johnst.) from Maine to New York without giving a description of his material.

T. despectus is known as occurring on ships' bottoms (Hecht, loc. cit.). It seems that it has been transported to the Mediterranean (Banyuls) and New Caledonia (Pruvot-Fol, loc. cit.). As the species does not vary much either in shape or colour (Löyning, 1927, p. 256), the localities outside the boreal region need not be questioned.

The place where the specimen was collected in the Bay of Santos is 5 km. distant from the roadstead, where the ships await their turn in the harbour of Santos.

Discussion of *Tergipes despectus*.

The irregular shape of the rhinophores (Fig. 200) of the present slug is evidently due to the not quite good state in which we received it. The reddish markings described by previous authors are sometimes wanting (Alder & Hancock, 1845, loc. cit.). As for the rest we have no doubt of our classification, although we had only one slug and could not examine the mandibles and the nervous system.

Of the six species of *Tergipes* listed by Bergh (1879, p. 571) only *T. edwardsii* Nordm. from the Black Sea seems to be valid (*id.*, 1892a, p. 1024). To judge from the woodcut in Leunis-Ludwig, *Synopsis der Thierkunde*, 3rd ed., v. 1 (1883) fig. 883 on p. 989, all pairs of cerata in *edwardsii* stand on equal levels, not alternating.

Bergh (1879, p. 572) said that the short penis of *T. despectus* "seemed unarmed". As far as we know he did not examine more than one specimen. Therefore his indication "penis inermis" (1892a, p. 1024) need not upset our determination; a cuticular spout of 20 micra may have been overlooked in dissection. Thiele it is true, included an unarmed penis in the diagnosis of the family Tergipedidae (1931, p. 545) and so does Pruvot-Fol (1954, p. 378). Her Tergipedidae however are so much restricted that they do not deserve a family of their own. Thiele's Tergipedidae are the Cuthonidae Odhner (1934, p. 278). In this family a cuticular tube on the tip of the penis occurs, e.g. in the genus *Catriona*, in *Embletonia pulchra* and *E. pallida* (Pruvot-Fol, 1954, p. 412: *Tenellia ventilabrum* Dal.).

FIGURES 199-208.

Tergipes despectus (Johnst.). (Figs 199-204.)

FIG. 199.—Lateral view of living slug.

FIG. 200.—Dorsal view of preserved specimen.

FIG. 201.—Radular tooth.

FIG. 202.—Two transverse sections of kidney, one 35 micra in front of other.

FIG. 203.—Diagram of reproductive organs.

FIG. 204.—Transverse section of same.

a—anus. b—ampulla. c—cnidosac. d—male atrium. e—vas deferens. f—foot. g—female gland mass. h—pericardium. i—intestine. j—female atrium. k—kidney. m—penial gland. n—renal pore. o—female follicles of ovotestis. p—penis. q—spermatheca. r—renopericardial canal. s—spermoviduct. t—male follicles of ovotestis. u—right liver branch. v—left anterior liver branch. w—left posterior liver branch. x—oviduct. y—nidamental ducts.

Embletonia evelinae, sp. nov. (Figs 205-208.)

FIG. 205.—Sketch of living slug.

FIG. 206.—Same, ventral view.

FIG. 207.—Diagram of reproductive organs.

FIG. 208.—Oblique transverse section of the anterior region.

a—anus. b—central nervous system. c—pericardium. d—digestive gland. e—vas deferens. f—female gland mass. g—gland of oral tube. h—pharynx. i—oesophagus. j—mouth glands. k—hermaphrodite duct. m—ampulla. n—oviduct. o—ovotestis. p—penis. q—prostatic part of vas deferens. r—renopericardial duct. s—salivary gland. t—spermatheca. u—fertilising duct. v—vagina. w—spermoviduct. x—male vestibule. y—nidamental opening. z—stomach. za—anterior diverticulum of stomach.

When Hoffmann (1933, fig. 84B) copied Alder & Hancock's fig 3 (1845) he was not aware of the note, that the figures of plate 36 had been reversed.

Mature slugs of *T. despectus* were observed with a length varying from 0.5 to 5 mm. (Löyning 1927, p. 256). Pruvot-Fol (1954, p. 379) also observed spawn of a small slug.

***Embletonia evelinae*, sp. nov. (Figs 205-212)**

The living slugs (Fig. 205) are slender, have a sole nearly as broad as the body and a long, pointed tail. They are colourless with a little black pigment and a yellowish-grey digestive gland. Their length is up to 3 mm. Preserved they are much stouter (Fig. 209), no more than 2 mm. long, and somewhat curved, the head downwards, the tail upwards. In preserved specimens the rhinophores are 0.4 mm., the cerata 0.8 mm. long. The sections are 0.5 mm. high and 0.45 mm. broad with a 0.21 mm. broad sole. The latter is entirely ciliated, the anterior border of the foot is notched but neither transversely grooved nor laterally produced. The rhinophores are thin and smooth, the veil small and round, without lateral expansions.

Each group of cerata consists of one ceras. The three or four cerata on either side of the body stand on equal levels. They are flask-shaped and broadest below the middle. The blunt free end has no pore and does not contain a cnidosac. The digestive gland (*d*) within the cerata is racemose in the middle and ends with a blind tube. Pink epidermal glands show in the terminal part of the ceras as in those of many nudibranchs.

The anus (*a*) together with the renal pore lies on a small papilla between the first and second ceras on the back. From there the kidney extends far backwards as a smooth tube. The heart (*c*) is inconspicuous, 0.15 mm. long in the sections. The three genital apertures lie on a level with the anus or a little behind it, but still in front of the second right ceras. The first is the male, that in the middle the vaginal (*v*) and the last the oviducal opening (*y*).

Clusters of glands (*j*) surround the mouth. The following quite short oral tube receives the long duct of a gland (*g*) located behind the pharynx (*h*) on the left side. This gland is a spherical vesicle surrounded by voluminous secretory cells. The short ducts of the salivary glands (*s*), the granular secretion of which stains red and blue, open into the dorsal cavity of the pharynx (*h*). The jaws are extremely delicate and smooth.

The radula (Fig. 210) is uniserial; the greatest number of teeth that was verified is 52. Adult teeth (Fig. 212) are approximately V-shaped and slightly curved. They have a weak median cusp and two to four strong lateral denticles on each side. As the position of these denticles varies, slanting converging rows are brought about along the radula (Fig. 210). The first tooth of the developing radula is still present even in our biggest specimens. It is a solid tooth, thrice as long as broad, has thickened borders (Fig. 211) and is somewhat similar to the adult radula of *Calma glaucoides* Ald. & Hanc. (Evans, 1922, pl. 11, fig. 4). The following plates increase regularly in size, especially in breadth.

The short oesophagus (*i*) leaves the pharynx behind and curves upwards. It opens into the bottom of the sac-shaped stomach (*z*). The latter forms an anterior diverticulum (*za*), the epithelium of which is low, like that of the rest of the stomach. The anterior part of the stomach is situated near the dorsal body wall and sends the right and left anterior hepatic diverticula into the pre-anal pair of cerata. Farther behind the short intestine leaves the dorsal wall of the stomach, runs upwards and opens with the anal rosette. Black pigment fills the connective tissue around the intestine. The stomach and the digestive gland continue backwards up to the region behind the last cerata, ending blindly a little in front of the hindmost follicles of the gonad. The limit between the stomach (*z*) and the digestive gland (*d*) lies approximately at the level of the second cerata. The epithelium of the stomach is flat, that of the liver more or less high and vacuolated. The contents of the vacuoles,

though of ovoid shape, are not nematocysts. The anterior liver ducts are very short, while those to the posterior cerata are long canals with high epithelial cells.

The hermaphrodite gland (*o*) consists of rather large sacs that are more or less subdivided. The female cells are principally peripheral, in part occupying superficial pouches as in *Tenellia pallida* (Marcus, 1955a, fig. 31). The separation of central male and peripheral female cells is however only approximate (Fig. 207). The longish ampulla (*m*) stretches from behind the genital pores to the front of the spermatheca (*t*). The spermoviduct (*w*) leaves the ampulla in the middle of the ventral wall, immediately in front of the entrance of the hermaphrodite duct (*k*), and bifurcates. The vas deferens (*e*) runs forward and becomes glandular, prostatic (*g*). Farther distally the duct is thin and muscular, winds and enters the anterior end of the penial papilla (*p*) which is strongly muscular. The same holds true for the male vestibulum, as is shown in the transverse section (Fig. 208, *x*). The penis is directed backwards and unarmed.

The female branch of the spermoviduct, the short oviduct (*n*), enters the female gland mass (*f*) that debouches with a wide, folded and ciliated oviducal opening (*y*). In front of it the ciliated vagina (*v*) extends inwards, gives off the uterine duct (*u*) to the gland mass (*f*) and opens into the spermatheca (*t*), an oblong organ that is located in front, beside the ampulla (*m*). The spermatozoa are fixed to the spermathecal wall by their heads.

Occurrence : Near Ubatuba, north-eastern coast of the State of São Paulo on *Obelia* grown on *Padina* and *Sargassum* in the upper littoral. About 20 slugs of all sizes were found on 10 and 11 September, 1955, but no spawn. We did not see the animals feed on Hydrozoa.

Discussion of *Embletonia evelinae*.

We agree with Pruvot-Fol (1954, pp. 410-412) who separates *Tenellia* A. Costa, 1866 with cnidosacs and more than one ceras to each group of cerata from *Embletonia* Alder & Hancock, 1851, without cnidosacs and only one ceras to each group. The genital organs are known in *Tenellia fuscata* (Gould) (Chambers, 1934), *T. pallida* (Ald. & Hanc.) (Marcus, 1955a) and *Embletonia evelinae*. The copulatory male organ has a cucumber-shaped appendix in the two species of *Tenellia*, while such is absent in *Embletonia*.

Tenellia pallida and *T. fuscata* differ in details of the reproductive organs (Marcus, 1955a, p. 241). The question how many species of *Tenellia* can be distinguished, and which is the valid name of *pallida*, may be left aside.

Embletonia comprises two species, *E. pulchra* (Alder & Hancock, 1844, p. 329; 1851, Fam. 3, pl. 38; 1855, text to pl. 47, Supplementary) and *E. faurei* Labbé (1923, p. 267). The latter, which was found on fish eggs, is insufficiently described, but cannot be identical with *evelinae*, because it has four anterior pairs of cerata distant from one another and five posterior pairs near together at the rear. *E. pulchra* differs from *evelinae* by two lateral expansions of the head, short rhinophores, simply tubular, not racemose hepatic tubules in the cerata, and two pairs of cerata belonging to the right and left anterior liver. The tip of the penis of *E. pulchra* seems to be cuticularized (Odhner, 1939, p. 75).

Phidiana selenkai, Bergh. (Figs 213-217.)

More specimens collected in 1954 make it possible to complete our earlier description (Marcus, 1955), as well as to compare *P. selenkai* with *P. lynceus* Bergh and *P. brevicauda* Engel. For the characters of the three first specimens of *P. lynceus* described in 1867 (*Dansk. Naturhist. Foren Vidensk. Meddel.* for 1866) we are restricted to Engel's detailed quotations (1925, pp. 55-72); the "*P. lynceus*, Bgh. var." (Bergh, 1874, pp. 615-618) came from Guadeloupe like the slugs of the first description which was evidently not modified but only amplified by this animal.



Besides *P. lynceus*, *P. selenkai*, and *P. brevicauda* two other Atlantic species are *P. patagonica* (d'Orb.) from the coast of Patagonia and *P. longicirra* Eliot from the Cape Verde Islands. Radula and penial armature of the first are not known; the colour differs from that of *selenkai*. The second has no denticles on the cusp of the radular tooth and no penial hook; the cerata are annulate.

The length of our new specimens of *selenkai* attains 18 mm. preserved, the tail is short and generally rolled up like a pig's tail, as in *brevicauda* (Engel, 1925, p. 68). The length of this tail is in none of the mature slugs more than one-sixth of the body length: often it is less. The same proportion was observed in living slugs, body length 35 mm., length of tail 5.5 mm. But it is dangerous to distinguish the species according to this proportion, because smaller animals have a comparatively longer tail, e.g. a 6 mm. long preserved slug had a 2 mm. long tail.

The breadth of our new preserved specimens attains 6 mm. in the pericardial region, the maximum height 6 mm., as in the animal previously described. Completely narcotized slugs are broader than high after fixation, and the same holds true for the living resting animal with the sole applied to a substratum. If a slug searches for support it stretches its foot and becomes high and narrow. The new animals have an average proportion of 3 : 1 between length and breadth corresponding to that of our first description. This proportion does not constitute a disjunctive character between *selenkai*, *lynceus*, and *brevicauda*. Only Bergh's single specimen of *selenkai* from Rio de Janeiro (1879, pp. 560-563), the biggest of all (22 mm. preserved), with the proportion 5.5 : 1 is isolated.

The colour of the living slug, which has not yet been described, is as follows: head white, powdered with orange; tentacles bright orange; upper perfoliations of rhinophores white, lower ones deep reddish-yellow; back very light orange with white middle streak over pericardium; flanks, foot, and tips of cerata white. The nodular liver tubes in the cerata are brown. They end with a black ring that is preserved after fixation. The same ring occurs in *brevicauda*. As the colour of living *lynceus* and *brevicauda* is not known, one cannot discuss the systematic value of this character.

Neither our former (17 series) nor our new (up to 24 series) slugs attain the number of 32 series of cerata described for Bergh's big specimen of *selenkai*. Our first specimen

FIGURES 209-222.

Embletonia evelinae, sp. nov. (Figs 209-212.)

FIG. 209.—Lateral view of alimentary tract. For lettering see Figures 119-208.

FIG. 210.—Radula.

FIG. 211.—First teeth of radula.

FIG. 212.—Later teeth of same.

Phidiana selenkai Bergh. (Figs 213-218.)

FIG. 213.—Living slug.

FIG. 214.—Transverse section of common ceras.

FIG. 215.—Same of ceras from canal between right liver and anterior right-sided left hepatic branch.

FIG. 216.—Diagram of kidney.

FIG. 217.—Diagram of reproductive organs.

FIG. 218.—Section of penis.

a—ampulla. *b*—blood sinus. *c*—renal canal. *d*—duct of spermatheca. *e*—vas deferens. *f*—female gland mass. *h*—pericardium. *i*—spermoviduct. *k*—kidney. *l*—liver diverticula. *m*—male atrial pore. *n*—renal aperture. *o*—oviduct. *p*—penis. *q*—female pore. *r*—renopericardial organ. *s*—spermatheca. *t*—stylet. *v*—male atrium. *w*—valve at outlet of ampulla. *x*—second male pore.

Cratena kaoruae, sp. nov. (Figs 219-222.)

FIG. 219.—Section of ceras.

FIG. 220.—Mandibles.

FIG. 221.—Masticatory border of mandible.

FIG. 222.—Radular tooth.

of 14 mm. body length had been fixed without previous narcosis. It has more cerata (245) than the two largest of the new slugs (18 and 16 mm. ; 224 and 242 cerata), but it may have been bigger than these when alive, and only more contracted when it was fixed. The left cerata of three examined new animals were a little more numerous than those on the right side, unlike those of our first slug. The rows of the cerata were more regular in several of the new slugs than in the previously described specimen. The middle area without cerata is a little broader than each of the lateral fields with cerata, when the anterior third of the body is examined. The posterior region where the median part becomes narrower is unimportant for the detail that distinguishes *selenkai* from *lynceus* and *brevicauda*. The lateral fields of *lynceus* occupy each about one-fourth of the whole breadth of the back (Bergh, 1874, p. 616) ; those of *brevicauda* are much narrower ("viel schmaler" Engel, 1925, p. 68) than the middle. The nine new slugs of at least 12 mm. body length (all preserved in the same way) have 18 to 22 right and 20 to 24 left rows of cerata. Bergh's bigger specimen of *selenkai* has some rows more, *brevicauda* some less, and *lynceus* approximately the same number. The character cannot be used for specific separation.

The location of the anus however shows differences that are of taxonomic value : it lies behind the second group of cerata in *selenkai* (Bergh, 1879, p. 560, and in our material) ; within the third group, separating it from a fourth, in *lynceus* (Bergh, 1874, p. 616) ; and between the hindmost rows of cerata in *brevicauda* (Engel, 1925, p. 69).

Sections of the cerata (Fig. 214) show two blood sinuses each with a strong sphincter at the base. The cerata that accompany the connecting canal between right liver and anterior right-sided branches of left liver (Fig. 215) have a thick opaque integument. This contains numerous large basophilic gland cells over a dense layer of connective tissue.

The tentacles do not contract very much when completely narcotized slugs are fixed and when preserved have a length up to 4.5 mm. Apart from this, our first description is sufficient with regard to the cephalic appendages. The tentacles were 8 mm. long in a 35 mm. long living slug. The semicircular disc at the anterior end of the foot (Bergh, 1874, pl. 9, fig. 4 : *lynceus* ; Engel, 1925, p. 67 : *brevicauda*) occurs also in some of the preserved specimens of the new material, the sole of which has undulating borders behind the expanded fore end.

The nervous system does not involve clear systematic characters, except the absence of pigment in the neurilemma (against *lynceus*). A short and thick connective, the so-called olfactory nerve, unites the massive rhinophoral with the cerebral ganglia. The cerebropleural ganglia are flat and concave in the dorsal mid-line ("reniform" Bergh, 1879, p. 561), where the short cerebral commissure connects the right and left half. A subcerebral commissure is developed. The elements which leave the pleural ganglia (visceral loop) and pedal ganglia (pedal commissure and possibly parapedal commissure) cannot be analyzed with certainty due to their common sheath of connective tissue. The cerebrobuccal connective is long but not thin as in *brevicauda* (Engel, 1925, p. 69) ; the buccal commissure is a little longer than the diameter of the buccal ganglia. The gastro-oesophageal-buccal connective is quite short ; the gastro-oesophageal ganglia consist of about five cells up to 90 micra in diameter. In the central ganglia the cells are up to 0.13 mm. in diameter ; Bergh (1898, p. 552) measured 0.16 mm. in *P. inca*.

The original description of *P. selenkai* gave about 25 to 30 denticles on the masticatory process of the mandible, our first specimen had between 20 and 25 denticles, the new material up to 26. This gives a difference against *lynceus* with 14 to 15 denticles, while *brevicauda* with "more than 20 denticles" cannot be distinguished by the masticatory structures. Taxonomically useless are the number of the radular teeth, that of their denticles, and the shape of the teeth. Engel (1925, p. 67), it is true, called the teeth of *brevicauda* "longer" than those drawn for *lynceus*, but the tooth of *brevicauda* (loc. cit., fig. 5 on p. 70) is folded at its base and therefore appears higher.

Minor differences of the shape of the teeth may be seen from the drawings, while that of *selenkai* (Bergh, 1879, pl. 6, fig. 13) shows perfect conformity with our material.

On the whole, the slight diversities in the configuration of the radulae cannot be summarised in the concise terms of diagnoses. The number of teeth of *selenkai* was 15 in our first specimen, 18 or 19 in our new and in Bergh's material, 16 complete and two developing teeth in *lynceus*, 13 or 14 and one not yet full grown in *brevicauda*. The denticles on each side of the cusp are: 4 or 5 in Bergh's *selenkai*, 3 to 6 in our first specimen, 4 or 5 in the present material, 3 or 4 in *lynceus*, and 4 to 6 in *brevicauda*.

The loose, clustered salivary glands lie between stomach and liver. The stomach contains hydroids and many cerata of other individuals of the same species. Cannibalism was also observed in species of *Facelina* (Alder & Hancock, 1845, Fam. 3, pl. 12; Trinchese, 1882, p. 41). *P. selenkai* agrees with Engel's indications (1925, p. 70) for *P. brevicauda* in respect of the short pharynx immediately followed by the folded stomach with an anterior hepatic duct on the right and one on the left side, and a posterior one on the left side, the posterior gastric dilatations to the front and to the left side which lie upon the anterior stomach, and the intestine described in our first report on *selenkai* (Marcus, 1955). The anus of the present specimens lies regularly between the fifth and sixth row of the second group of cerata.

The diagram of the kidney (Fig. 216), the ramifications of which have been omitted, shows that this organ agrees with *P. brevicauda* (loc. cit.), not with *P. inca* (Bergh, 1898, pp. 556-557). The voluminous renopericardial communication (*r*) contains four folds and joins the renal sac (*k*) far behind by a long thick-walled canal (*c*). Another canal passes from the kidney to the right side where it opens with a wide, rosette-shaped aperture (*n*) that lies on the level of the canal between anterior right and anterior right-sided left liver.

The reproductive organs (Fig. 217) correspond to the general scheme for the genus (Engel, 1925, p. 67); the spermatheca (*s*) is as Bergh (1879, p. 562) described, nearly reniform, its duct (*d*) longer than the vesicle and connected with the entrance of the oviduct (*o*) into the female gland mass (*f*).

The hermaphrodite gland contains mixed and separate follicles, the female ones on the whole more peripheral, the male ones more central. The spermoviduct (*i*) is dorsomedian; the coiled ampulla (*a*) has muscular walls and a ciliated lining, and contains masses of irregularly-heaped sperm. The ampulla ends with a fold (*w*) which seems to regulate the outflow of the germ cells, though its function is not as obvious, as that of the hermaphrodite valve in *Archidoris montereyensis* (McGowan & Pratt 1954, p. 263, pl. 1, fig. 1, *v*; pl. 2, fig. 7). The efferent duct (*e*) is muscular and has a high, red-staining glandular epithelium. The duct widens where it enters the voluminous penis (*p*) which is surrounded by the male vestibulum (*v*), also muscular. Basophil and eosinophil glands occur in the epithelia which line the vestibulum and cover the penis. The vas deferens opens at the tip of the stylet (*t*), the measurements of which agree with those of our first specimen. The obliquely truncate opening of the stylet is about 20 micra long. There are slight variations of length, diameter, and angle of the cusp in the three specimens, the penis of which was examined. They have all a second opening (Fig. 218, *x*) of the efferent duct at the base of the stylet. This opening can be seen in the dissected penis in alcohol, and was correctly observed by Bergh (1874, p. 618, pl. 9, fig. 12*a*) in *P. lynceus*. Later he questioned this statement (1879, p. 562, note 1), and Engel also (1925, p. 35) thought that the second pore was due to injury.

The long, ciliated oviduct (*o*), simplified in the diagram like the male duct, bends in an acute angle and communicates with the broad female gland mass (*f*) by more than one opening. The duct (*d*) of the spermatheca has ciliated and folded epithelium and opens into the middle of the vesicle (*s*). Here the spermatozoa lie all in the same order, the minute heads directed to the wall, forming a continuous blue line, and the tails in parallel waves (McGowan & Pratt, 1954, p. 265). The female gland mass (*f*)

is folded and stains diversely, has mucous and granular parts, and opens (*g*) a little below and behind the male atrium (*m*).

Occurrence : Under stones in the lower tidal zone of several localities at Ubatuba, in the bay of Santos, and near Itanhaen, 50 km. south-west of Santos ; 30 specimens. July to December 1954.

Discussion of *Phidiana selenkai*.

P. selenkai must be maintained with its separate name ; whether as species or as subspecies is without importance. Its cerata-bearing fields are relatively broader than in *lynceus* and *brevicauda*, and its anus lies farther in front. Moreover it differs from *lynceus* by the non-pigmented neurilemma and the number of denticles on the masticatory process, in a somewhat vague degree also by the shape of the stylet.

If Odhner's system (1939, p. 53, 77) is adopted, *Phidiana* has its place among the Facelinidae, Facelininae.

Cratena kaoruuae, sp. nov. (Figs 219–224.)

Living and completely extended slugs attain 9 mm. in length ; the notum is about 1 mm. broad, the foot 2 mm. in an 8 mm. long living slug. The breadth of the body decreases evenly from the fore to the hind end. The foot projects on the sides ; its anterior angles are strongly produced and limited by a constriction immediately behind them.

The slender, nearly cylindrical cerata are disposed in 6 groups. The first three are horseshoe-shaped, the three hinder ones oblique rows. The biggest slug has ten cerata in the first group, eight or nine in the second, seven in the third, six in the fourth, five in the fifth, and three in the sixth. As usual, smaller slugs have less appendages. The cerata of the living slug are up to 3.2 mm. long and 0.2 mm. in diameter. Their size seems to vary in various animals, as Miss Hosoe drew the medial cerata of her living slug smaller than the more lateral ones, contrary to what is found in the preserved specimen that she gave us. Perhaps the inner cerata of her drawn slug were all in regeneration. The genital openings lie near together within the first horseshoe, the renal pore in front of and the anus within the second.

The animals are of a transparent ivory colour with an orange hue. Orange pigment lies principally on the sides of the head. Brown pigment is more or less frequent in the three specimens, but always scarce ; the hepatic diverticula of the cerata are dark brown. The cnidosacs are whitish as generally. Opaque white spots occur all over the body, with a concentration on the dorsal surface of head, tentacles, and rhinophores.

The black eyes are 60 micra in diameter ; the length of the tentacles is 3 mm., that of the rhinophores 2.8 mm. in a living slug of 8 mm. length. The rhinophores are covered with small tubercles but neither annulated nor perfoliated.

The mandibles are relatively thick and have distinct lines parallel to the border. The anterior margin is folded, the dorsal is concave (Fig. 220). The masticatory process is strong, broad, and distinctly set off ; its margin is serrated and bears 38 slightly irregular denticles. The radula consists of twelve or thirteen teeth. The median cusp is four times bigger than the lateral denticles, the number of which is two to five on each side. The number of these denticles varies in the radula without relation to the age of the plates, there may also be different numbers on both sides of one plate changing from side to side.

The oesophagus is wide and longitudinally folded, the stomach ample and thin-walled, the gut ciliated and muscular. The latter contained cuticular elements of Crustacea and their undigested embryos, which had perhaps been swallowed as gastric contents of Hydrozoa. The slightly undulating liver tubules in the cerata communicate with the cnidosacs by a simple, not glandular, canal.

The male genital pore is covered with cutaneous folds. The vas deferens opens subterminally on the blunt tip of the penis and winds as a narrow canal to the root of the latter. There the duct dilates and is lined with red-staining prostatic gland cells. The muscular penis itself is about 0.5 mm. long and 0.4 mm. in diameter in retracted position. The ental two-thirds of its length are covered by a dorsal flap, and its ental half is coalesced with the dorsal wall of the atrium. In one of the present two series of sections an indistinct spiral furrow runs around the copulatory organ (Engel, 1925, fig. 15a, F), which was not observed in the other. Both series show a cavity at the root of the penis separated from that of the atrium by a constriction. Like the inner lining of the atrium the border of this constriction is glandular. Evidently this hollow organ corresponds to what Engel (1925) observed at the base of the penis of *Caloria occidentalis* (fig. 15, o). The efferent duct ental to the penis forms a thick coil that lies between the atrium and body wall in both series, and remains glandular up to its separation from the oviduct.

The female pore lies about 0.1 mm. behind the male opening. In one of the series the ectal part of the oviduct is dilated by a plug of sperm evidently introduced shortly before the slug was preserved. One of the slugs with completely developed male and female efferent organs had no gonad, which must have degenerated. The other had an ovotestis in incipient male phase. As the twisted ampulla of this slug contains ripe sperm, the numerous spermatogonia indicate that the production of male germ cells is repeated. The communication of the spermatheca with the female duct could not be analyzed.

Occurrence : Cananéia, 200 km. south-west of Santos, in a lagoon of very variable salinity (14–26.5 per mil. after Vannucci & Hosoe, 1953, p. 103). 3 specimens collected by Lic. Kaoru Hosoe (now Mrs. Moriguchi) who drew Figs 223 and 224 and furnished the sections and the data that refer to the living animals.

Discussion of *Cratena kaoruæ*.

Cratena peregrina (Gmelin, 1791), Bergh's type (1864) of his genus, differs from the present species by its colour pattern (Bergh, 1883a, p. 37; Vayssiére, 1913, p. 284; Pruvot-Fol, 1948, p. 275; 1954, p. 399). Macnae (1954, p. 9) includes *Hervia lineata* Eliot, 1904 and *H. serrata* Baba, 1949 in *Cratena*, both of which are different from *kaoruæ* in colour and radula. As Odhner remarked (Macnae, loc. cit.), the radula of Baba's species (1949, fig. 1, 143B) is like that of *Favorinus*, but the masticatory process has only a single row of denticles. In a further *Cratena*, *C. capensis* Barnard, 1927, only the first groups of cerata are horseshoe-shaped. According to Macnae possibly *Hervia berghii* (Vayssiére, 1888) also belongs to *Cratena*. Its radular tooth has up to 8 lateral teeth (Vayssiére, 1928, *Hervia Berghii*, fig. 4), and its colour pattern does not agree with that of *C. kaoruæ*. The shape of the anterior liver groups is not clear from the figures of *H. berghii*; probably this species is a young *Facelinid*, viz. *Acanthopsole rubrovittata* (Pruvot-Fol, 1951, p. 56, 64; 1954, p. 392: *Facelina*). The two species from New Caledonia, *Hervia ducrosi* and *H. trunca* (Risbec, 1928, pp. 232, 236; 1953, p. 135) are probably *Cratena*; their radulae differ widely from *C. kaoruæ*. In the first of these species the worn radular teeth are said to accumulate in an ascus.

The new species resembles *Caloria occidentalis* Engel (1925, p. 73) in several features. The liver horseshoes with more than one row of cerata in each limb and the annulated rhinophores exclude the Jamaican species from *Cratena* in its modern, restricted sense (Macnae, 1954, pp. 8, 29). It belongs to the Rizzoliinae Odhner (1939, p. 77), to-day again called *Favorininae*, as well as *Caloria guenanti* (Risbec, 1928, p. 244; 1953, p. 155) and *Facalana pallida* Bergh (1888, p. 784). However the type of *Caloria*, *C. maculata* Trinchese, 1888, and *C. australis* (Risbec, 1937, p. 162; 1953, p. 156) are *Facelininae* (Odhner, 1939, fig. 44).

It is true that the distribution of the papillae was not figured by Trinchese, whose paper we owe to the kindness of Professor Dr. Floriano Papi (Pisa). But we agree

with Engel that Trinchese would have described the "cuscinetti" as like "la forma di ferro di cavallo" (1882, p. 72 : *Favorinus branchialis*) if this type occurred in his species. However in the general as well as in the detailed description he speaks of "serie trasversali". The genital opening of *Caloria maculata* lies near the hind end of the first group of cerata, the anus under the outer border of the second cushion, between the first and second series of papillae. Its rhinophores are provided with scattered "lievi ripiegature" and "rughe irregolari". Bergh (1890, p. 39 ; 1892*a*, p. 1033) and Thiele (1931, p. 469) called them annulated, Vayssière (1913, p. 274) "plissés" and Pruvot-Fol (1948, p. 274 ; 1951, p. 60) "lisses" or "simples" (*ead.* 1954, p. 397). The rhinophores are indeed variable in the Facelinidae (Meyer & Möbius, 1865, p. 28 ; Bergh, 1886, p. 41) and therefore do not furnish secure generic characters in this family. Löyning (1922) observed in a *Facelina* that Odhner (1939, p. 80) says *F. auriculata* (O. F. Müll.) has hardly annulated rhinophores in young (Löyning, 1922, pl. 3, fig. 10*d*) and distinctly perfoliated ones in old slugs (*ibid.*, text-fig. 24). Baba (1949, p. 102, 177) described a species of *Favorinus* with perfoliated rhinophores, which are quite unusual in this genus.

After Pruvot-Fol (1951, p. 56 ; 1954, p. 392) *Hervia berghii* (Vayss.) with smooth rhinophores passes to *Facelina rubrovittata* A. Costa, 1866 with annulated ones.

Nanuca gen. nov.

Small Facelinidae with a simple right liver (Favorininae) forming a narrow arch. Other liver branches similar. Anterior end of foot a thickened glandular disc. Rhinophores annulate. Jaws with a single row of denticles on masticatory edge. Central cusp of radular tooth markedly longer than lateral denticles. Penis unarmed, folded. Without heart or kidney.

Type of the genus : *Nanuca sebastiani* sp. nov., named for Dr. Sebastian A. Gerlach (Kiel) who collected the slugs at Recife.

The Facelinidae of the preceding diagnosis are understood as cleioproct Aeolidacea with cuspidate radular tooth and an anus located in the second group of cerata (Odhner, 1939, p. 53). The genus belongs to the Favorininae with only one row of cerata in each limb of the hepatic horseshoes or in each branch (*Herviella*). Besides *Favorinus* Gray and *Pteraeolidia* Bergh with several series of denticles on the masticatory border of the mandibles, *Cratena* Bergh, *Herviella* Baba, and *Amanda* Macnae are the genera certainly belonging to this group. None of them has the liver branches as much reduced as the new species, the small size of which is evidently correlated with the loss of heart and kidney.

Nanuca sebastiani sp. nov. (Figs 225-233.)

The four preserved slugs were 1.5 to 2.5 mm. long, but the hind end was complete only in the smallest of them. The breadth is up to 0.6 mm., and so is the height. The foot is a little narrower than the back. From the head, which is broadest, the body tapers backwards. The finger-shaped tentacles (*t*) are smooth, about 0.4 mm. long, the rhinophores (*u*) shorter and annulated with three or four complete rings. The widened anterior border of the foot (*g*) is broadly rounded, and the sole is glandular. The cerata are up to 1 mm. long ; they are not stalked and stand in groups that may be considered as horseshoes. The present material shows at most three groups, perhaps because the hind end of the bigger specimens is wanting. The right liver forms one group, the left liver one anterior, and on each side two posterior groups. There are no more than four cerata and a minute primordium of a fifth in one group. The cerata are nearly club-shaped and broadest beyond the middle ; the cnidosac tops the ceras as a colourless bulb. The colour is only known from the preserved specimens which were dirty brownish with a darker liver.

The genital pore (*w*) lies under the first group of cerata, the anus a little ventral to the second. Since there is neither heart nor kidney, a nephroproct is absent.

The outer surface of the labial disc (Fig. 229) which surrounds the inner mouth bears a smooth cuticle. An inner ring of radial dilators and an outer one of retractors insert on its ental surface. The jaws are colourless with thickened borders and about 18 denticles on the edge of the masticatory process, which increase in size backwards. The radula consists of up to 14 horseshoe-shaped teeth. Their cusp is long, strong, and accompanied by two to four denticles on each side.

The stomach is large, and the liver tubules in the cerata are smooth. The gastric and hepatic lumen contain free nematocysts, which are intracellular in the cnidosacs, where two types of about 20 micra and 4 micra can be distinguished.

The male and female follicles of the ovotestis (*o*) seem to be separate. The ampulla (*a*) lies between ovarian follicles. The ciliated efferent duct (*e*) emerges from the female gland mass (*f*). After passing through a sphincter (*s*) it becomes thick and glandular (*g*) and curves to the male antrum (*x*). The latter surrounds the lobate and fleshy pleurembolic penis.

The female antrum opens close to the male one on a common prominence. The female duct (*v*) functions as vagina and as oviduct (nidamental duct). The rather long canal of the sausage-shaped spermatheca (*b*) begins far entally.

Occurrence : Recife, State of Pernambuco, Praia da Piedade, 4 specimens among calcareous algae from the outer side of the reef quite near the surface ; December 1954.

Spurilla neapolitana (Chiaje) var. *braziliana* MacFarland. (Figs 234-236.)

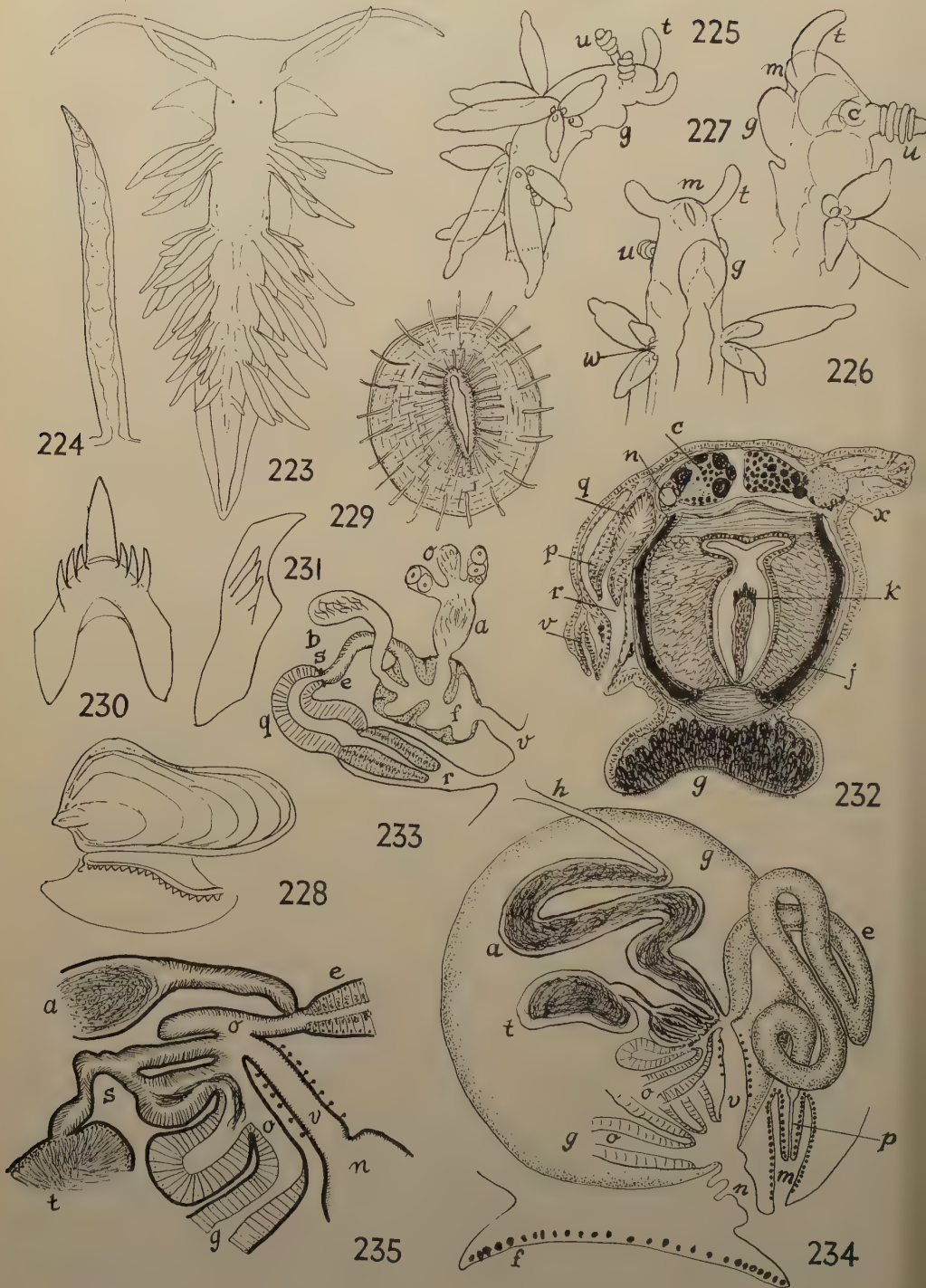
The reproductive organs of this form were summarized without figures in the previous description (MacFarland, 1909, p. 98). Now we have sectioned and reconstructed those of a slug about 16 mm. long. Their general topography had already been compared with that of other species of *Spurilla* and found quite similar (MacFarland, loc. cit.). Dissection of compact reproductive organs, as occur in the Eolidacea, rarely gives a plain idea of the connection of the various tubes (Eliot, 1910, p. 59 and note 2). Probably taxonomy would profit by a more general practice of microtome sections in the study of the reproductive organs of nudibranchs.

The ovotestis is paired, as stated by Bergh (1877, p. 761 ; 1883*a*, p. 18), in its middle part, while the smaller posterior (ental) and anterior (ectal) mass is undivided. The lobes are composed of numerous follicles. One or two peripheral layers are purely female, the central follicles are male, but their walls contain single bigger cells, evidently oocytes. There are no spermatozoa in the outer follicles.

The spermoviduct (*h*) is about 0.5 mm. long. The beginning of the ampulla (*a*) is dorsal to the gland mass (*g*) and lies 0.25 mm. in front of its hind end. From there the ampulla runs 0.4 mm. backwards and then bends forward. In this anterior course the ampulla is embedded in the female gland mass which is folded, not smooth as in the simplified figure. As in other species the wall of the gland mass stains differently in the various parts, and its cells contain blue mucus and coarse and fine red granules.

Four different ducts lead from the ectal opening of the ampulla, the male duct (*e*), the oviduct (*o*), the spermathecal duct (*s*) and the vagina (*v*).

The vas deferens (*e*) is almost uniformly thick from its beginning to its entrance into the penis (*p*). The ciliated epithelium contains red-staining glands. The cells are about 60 micra high and have big nuclei in the ental and middle part of the duct. The outer course of the duct is characterized by cells 0.1 mm. high with nuclei ten times the volume of the former. The calibre of the vas deferens diminishes suddenly at the root of the penis (*p*), so that the ejaculatory duct which runs through the pleurembolic copulatory organ is narrow. Our measurements of the latter, length 0.6 mm., diameter 0.3 mm. at the root, length of male atrium (*m*) about 1 mm., are considerably less than Bergh's (1883*a*, p. 18), but he dissected a slug more than twice



as big as ours. Voluminous cyanophil glands accompany the walls of the penis and the male vestibulum.

The female germ cells are led out by the oviduct (*o*) that opens into the female gland mass (*g*) and communicates with the strongly ciliated spermathecal duct (*s*). The cilia of this duct are 15 to 20 micra long. It consists of two or more irregular wide canals which contain sperm and unite before it enters the flattened spermatheca (*t*), in which the spermatozoa lie with their heads to the wall. Opposite the outer opening of the spermathecal duct is the inner orifice of the vagina (*v*), a muscular canal with cyanophil glands in its inner course. Its outer aperture debouches together with several nidamental ducts, functionally continuations of the oviduct, into the folded and ciliated female atrium (*n*).

We give drawings (Fig. 236) of four positions of anus (*u*) and renal pore (*i*) chosen from 20 slugs. Important is the distinctly abanal position of the nephroproct in *D*, where it is separated from the anus by cerata of the second group. This type shows that Aeolidiidae and Spurillidae cannot be distinguished by their abanal or adanal nephroproct.

Spurilla neapolitana braziliana is together with *Phidiana selenkai* Bergh the most frequent species of the Eolidacea under stones in the upper littoral of the State of São Paulo. We have found both species in the same biotope (Ubatuba), but more frequently either one or the other was seen in a particular locality. It seems that *Phidiana selenkai* penetrates more into such ecological niches, where the waves deposit great quantities of fine sand.

Berghia coerulescens (Laur.). (Figs 237-246.)

The living slugs of the present material are 12 to 20 mm. long, 3 to 4 mm. of which belong to the tail. The breadth of the foot is 3 mm., the height of the body 2 mm. The length of the cerata is 2 to 4 mm., that of the tentacles 3 mm., and that of the rhinophores 2 mm. The proportions that Engel (1925, p. 55) considered as taxonomi-

FIGURES 223-235.

Cratena kaoruæ, sp. nov. (Figs 223-224.)

FIG. 223.—Living slug, drawn by Miss Kaoru Hosoe.

FIG. 224.—Ceras of living slug, drawn by Miss Kaoru Hosoe.

Nanuca sebastiani, gen. et sp. nov. (Figs 225-233.)

FIG. 225.—Preserved slug.

FIG. 226.—Fore end of same from below.

FIG. 227.—Same seen from left side.

FIG. 228.—Jaw and labial disc.

FIG. 229.—Labial disc.

FIG. 230.—Radular tooth.

FIG. 231.—Same seen from side.

FIG. 232.—Combined transverse section of fore end.

FIG. 233.—Diagram of reproductive organs.

a—ampulla. *b*—spermatheca. *c*—brain. *e*—vas deferens. *f*—female gland mass. *g*—anterior end of foot. *j*—jaw. *k*—radula. *m*—mouth. *n*—statocyst. *o*—ovotestis. *p*—penis. *q*—prostatic part of vas deferens. *r*—male atrium. *s*—sphincter of vas deferens. *t*—tentacle. *u*—rhinophores. *v*—female opening. *w*—genital aperture. *x*—rhinophoral ganglion.

Spurilla neapolitana braziliana MacFarl. (Figs 234-235.)

FIG. 234.—Diagram of reproductive organs.

FIG. 235.—Detailed reconstruction of centre of genital ducts, simplified.

a—ampulla. *e*—vas deferens. *f*—foot. *g*—female gland mass. *h*—spermoviduct. *m*—male atrium. *n*—female atrium. *o*—oviduct. *p*—penis. *s*—spermathecal duct. *t*—spermatheca. *v*—vagina.

cally important were taken from a 12 mm. living slug : height to length 1 : 6, breadth to length 1 : 4, length of tail to total length 1 : 3.5.

The foot stands out with a lateral brim, its anterior border has a narrow furrow (*g*) and in some specimens a cleft, in others an entire upper part ("lip"). The lateral corners are long, the hind end is a pointed tail. There are numerous blue-staining sole glands. The tentacles are long and slender, the rhinophores more or less claviform, smooth on the anterior, pearly on the posterior side.

The spherical tubercles of the rhinophores do not form distinct oblique rows, nor are there conical bands, the "lamine olfactive" (Trinchese, 1882, p. 21) on the anterior side. Hoffmann (1933, p. 214) and Pruvot-Fol (1953, p. 57) have already discussed the different descriptions of the rhinophores. That of Bergh (1883a, p. 21) was qualified as indistinct ("undeutlich", Engel, 1925, p. 51); possibly it does not refer to *Berghia coerulescens* at all, but perhaps to an *Aeolidiella*, as is suggested by the many-branched right liver.

The cerata are arranged in 6 to 10 groups on each side; the anterior ones are horse-shoe-shaped arches, several posterior ones are simple. The foremost arch contains about ten cerata in a 12 mm. long slug; backwards the number decreases to two. Our biggest slug has from twenty-one to two cerata, a total of 74 cerata on one side.

The animals are bluish-white with brown liver and a yellow and red skin pattern. The slug from Santos had yellow tips of tentacles and rhinophores, a yellow dorsal mid-line from the second group of cerata to the tip of the tail, four large yellow dorso-median spots between the first and second arches, one yellow triangle between the eyes and a yellow spot in front of them. Two oblique orange lines extend from behind the rhinophores to near the four yellow spots. Red marks are two lines between tentacles and rhinophores and a complete ring around each cnidosac. The bases of the rhinophores are pink. The slugs from Ubatuba (Fig. 237) agree with the specimen from Santos in yellow tips and tentacles and rhinophores, two red lines between their bases, two orange oblique lines behind the rhinophores, and a red ring around the cnidosac, sometimes restricted to the upper surface. Further colour marks are: red bases of tentacles and rhinophores and two dorsolateral red lines along the whole back which border the insertions of the cerata as in Pruvot-Fol's pl. 1, fig. 11 (1953).

The genital apertures (*g*) lie close together in the first arch of cerata; the anus (*a*) lies in the second arch (*c*), sometimes near the cerata of the posterior limb, occasionally near those of the anterior (Fig. 245). The renal pore (*r*) is pre-anal; its distance from the anus varies from 0.1 to 0.3 mm.

FIGURES 236-246.

Spurilla neapolitana braziliiana MacFarl. (Fig. 236.)

FIG. 236.—Four positions of anus and nephroproct.
i—renal pore. *u*—anus.

Berghia coerulescens (Laur.). (Figs 237-246.)

FIG. 237.—Dorsal view of living slug from Ubatuba.

FIG. 238.—Liver system of slug from Santos.

FIG. 239.—Rhinophore, lateral view from living slug (Santos).

FIG. 240.—Back of preserved rhinophore (Ubatuba).

FIG. 241.—Anterior end of three preserved slugs from below (Ubatuba).

FIG. 242.—Jaw with border of masticatory process (high power).

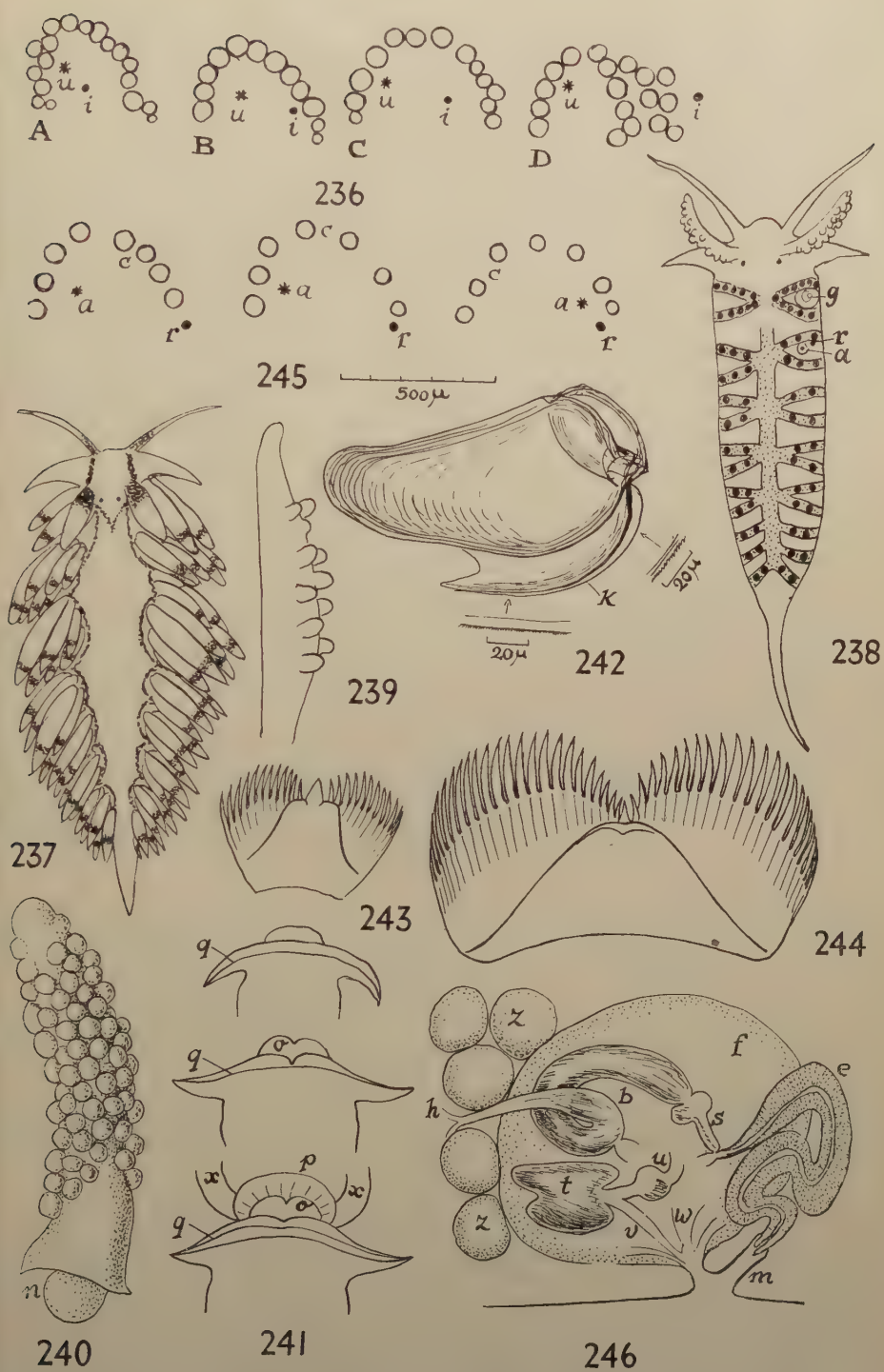
FIG. 243.—One of the oldest radular teeth.

FIG. 244.—Radular tooth formed in full-grown state.

FIG. 245.—Topography of anus and nephroproct in three slugs (Ubatuba).

FIG. 246.—Reconstruction of reproductive organs.

a—anus. *b*—ampulla. *c*—cerata of second arch. *e*—vas deferens. *f*—female gland mass. *g*—genital apertures. *h*—hermaphrodite duct. *k*—masticatory border of jaw. *m*—male atrium. *n*—rhinophoral ganglion. *o*—lower oral lip. *p*—upper oral lip. *q*—transverse furrow of anterior border of foot. *r*—renal pore. *s*—spermoviduct. *t*—spermatheca. *u*—fertilising duct. *v*—vagina. *w*—outlets of gland mass. *x*—tentacle. *z*—ovotestis.



The oral tube is cuticularized. The longish, mussel-shaped jaws (Fig. 242) have a long and broad masticatory process, the margin (*k*) of which appears smooth when low power (up to $\times 100$) is employed. Minute denticles are seen on the border with higher power ($\times 250-300$). The teeth of the radula are narrowed in the centre, broadened on the sides, and provided with a yellow transverse thickening. Glands of the oral tube with coarse red-staining secretion open with narrow ducts in front of the jaws and extend to the ovotestis. In *B. norvegica* these ptyaline or anterior salivary glands do not occur (Odhner, 1939, p. 87). Trinchese did not see posterior or true salivary glands in *B. coerulescens* (1882, p. 14). They do, however, exist; their secretion is fine and blue-staining. Their ducts run along the sides of the oesophagus and open on both sides of the radular cushion. The walls of the stomach are folded. The hepatic ducts of the right liver and its left partner leave the anterior part of the stomach. The intestine arises from the dorsal anterior wall and has a small ciliated caecum near the pylorus. The posterior liver goes dorsally out from the hind end of the stomach and extends in the mid-line of the back to the beginning of the tail. No nematocysts were seen in the hepatic cells, but long and slender ones in the cnidosacs. The cells that we considered as reserve material for regeneration of lost cerata in *Stiliger talis* Marc. occur also in the present species.

The kidney begins with two dorsolateral branches behind the anterior hepatic diverticula. The renopericardial duct lies between the first and second right arch, in front of the nephropore. The kidney becomes unpaired behind the anus and extends backwards nearly as far as the liver. The heart begins on a level with the kidney and ends on the level of the anus.

The ovotestis (*z*) consists of many small follicles that are united to bigger sacs. The male germ cells lie principally in the centre, the female ones on the walls of the acini. The ductules of the bigger sacs unite and form the hermaphrodite duct (*h*) which dilates and enters the female gland mass (*f*) as a winding ampulla (*b*). The folds of the gland mass surround the ampulla, the spermoviduct (*s*), the vagina (*v*) and the spermatheca (*t*). One communication exists between the ampulla and the lumen of the gland mass and probably a second between the latter and the spermoviduct near the origin of the vas deferens (*e*). The male duct is thick and glandular along nearly its whole length. It ends with an unarmed papilla in the male atrium (*m*). Near the atrial pore open several outlets (*w*) of the female gland mass, oviducts or nidamental ducts. The vagina (*v*) leads to a spermatheca (*t*) of irregular shape; the uterine duct (*u*) has a spermatocyst-like dilatation.

Occurrence: Bay of Santos, Ilha Porchat, 1 slug in September 1954. Ubatuba, on the north-eastern coast of the State of São Paulo, 5 animals under stones, above the low-water line; December 1954. One slug 16 mm. long was observed depositing its egg ribbon that is similar to that of *Spurilla neapolitana braziliana* MacFarl.

Further distribution: West Indies, Tobago Island (Engel, 1925, p. 52); Mediterranean; Atlantic coast of Morocco (Pruvot-Fol, 1953, p. 57) and France, northward to the French Channel coast (Cuénot, 1927, p. 262).

Records from Portugal are not known, as little as from the English side of the Channel (Eliot, 1906, p. 334). Bergh's specimens from the Adriatic (1883a, p. 20) have a many-branched right liver and probably do not belong to *Berghia coerulescens*.

Discussion of *Berghia coerulescens*.

As we have found *Spurilla neapolitana braziliana* with abanal nephroproct, the separation of the Cleioprocta with pectinate radula into two families must be abandoned. The variation of the distance between anus and renal pore in the present species confirms this view. Three of the genera with perfoliated or tuberculated rhinophores, *Spurilla*, *Berghia* and *Baeolidia* are closely related with one another (Odhner, 1939, p. 88), specially *Berghia* and *Baeolidia*, as Bergh observed (1888, p. 778). The type, *B. moebii*, has a broader furrow of the anterior pedal border and a deeper notch in the upper half of this border than is hitherto known in *Berghia*, but these characters

were not mentioned in Baba's diagnoses (1949, p. 184). The nearly uniform breadth of the radular tooth shown by Bergh's, Baba's, and Pruvot-Fol's (1953, text-fig. 17e) drawings characterizes *Baeolidia*.

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**THE EVOLUTION OF ARTHROPODAN LOCOMOTORY MECHANISMS.
PART 6. HABITS AND EVOLUTION OF THE LYSIOPETALOIDEA
[DIPLOPODA], SOME PRINCIPLES OF LEG DESIGN IN DIPLO-
PODA AND CHILOPODA, AND LIMB STRUCTURE OF DIPLOPODA.**
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(With Plate 9 and 21 text-figures.)

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INTRODUCTION.

A study of habits and locomotory mechanisms in terrestrial Arthropoda has already indicated the functional significance of some 50 salient morphological features of the trunk region. These structures include the diagnostic characters of major classes such as Diplopoda, Chilopoda, Pauropoda and Symphyla, and of their component orders. Such far-reaching interpretations had not been anticipated; they are of importance in enabling us to understand the manner of evolution of the several groups, and they throw light on taxonomic characters which hitherto have had no more than classificatory significance for us.

It was possible to present a much fuller interpretation of the morphology of the Diplopoda (Parts 4 and 5) than of the Chilopoda (Part 3) because of the comparative simplicity of the musculature of diplopods where the trunk muscles can be considered independently from those of the legs, and because of the wider variety of external form within this group. In the Chilopoda extrinsic leg muscles are numerous, extending to all major scutes, and neither the limb muscles nor those of the trunk can be considered independently, and there is no existing description of the entire musculature of even one chilopod. To further the interpretation of diplopodan structure, and to advance our understanding of the Chilopoda and Symphyla on similar lines, it has been necessary to study the anatomy and movements of the limbs of Diplopoda and Chilopoda in order to ascertain the principles of leg design.

The existing descriptions of the legs of myriapods are both incomplete and misleading, and except for Silvestri (1903), who described the limb musculature of diplopods on a functional basis, little attention has been paid to function. The principles of leg design which have emerged from a study of Diplopoda and Chilopoda are given below (section II), followed by a more detailed account of the correlations of limb structure with function in the Diplopoda (Sections III and IV). A corresponding functional account of the Chilopoda will follow in Part 7, together with a comparative survey of trunk musculature and its evolution in the main orders. From this detail the exact significance of conspicuous features such as heteronomy in tergite length, pleuron structure, type of spiracle and respiratory system, the peculiar forms of the coxa and trochanter etc. is apparent. This work is an essential preliminary towards an understanding of the manner of evolution of the Symphyla and Insecta, and an appreciation of the characteristics of the various hexapodous arthropods living on land.

Data derived from living representatives of the major orders of Diplopoda have been presented in Parts 4 and 5. Additional data of the habits of *Polyxenus* have been recorded by Schömann (1956). Four further animals, *Callipus longobardius*, *C. foetidissimus* and *Dischopetalum illyricum*, fleet carnivorous members of the Lysiopetalioidea, and *Dolistenus savii* have been obtained alive for the present work. On the classification of Attems (1926) and adopted here (see Part 4, p. 301), the Lysiopetalioidea form a well defined group among the Nematophora. As anticipated, these animals differ in structure and in performance from other Diplopoda, and with the Chilopoda clearly indicate the requirements of a leg providing speed, irrespective of unlike basic morphologies due to widely separated taxonomic positions.

METHODS.

Most of the methods employed have been described in previous Parts. Electronic flash illumination has been used for photography of leg movements. Muscle morphology has been ascertained mainly from whole or partial preparations, permanently mounted in balsam or cleared in benzyl alcohol and examined in fluid. A geological

microscope and polaroids attached to a dissecting binocular microscope have been of great value. Well-fixed material which has been stored for some time in alcohol is easier to use than fresh material for the study of muscle anatomy. Manipulation of narcotized living specimens has been of service.

HABITS, LOCOMOTION AND SYSTEMATIC POSITION OF THE LYSIOPETALOIDEA.

Data concerning habits and locomotory performance of the major groups of Diplopoda have been given in Parts 4 and 5 except for the Lysiopetaloidea. That these animals must be fleet was deduced from Löhner's photographs (Part 4), and the records of their carnivorous rock-living habits were contrasted with those of other diplopods. Two species have been obtained alive from the Gorizia region in north Italy, *Callipus longobardius* 42 mm. and *Dischopetalum illyricum* 31 mm. (Pl. 9, figs 24, 25, 28, 29 and 33) and *Callipus foetidissimus*, from Sicily. Speeds of running and pulling capacities were recorded at the site of capture, as well as in England.

General habits and use of coxal sacs.

Callipus longobardius and *Dischopetalum illyricum* were all found clinging to the underside of rocks, "am Bergabhang" (Verhoeff, 1910), and in captivity they rested in this position under stones and not on the soil surface. At no time did they burrow into the soil of a terrarium. They did not emerge during the day-time, and after a good meal an animal would stay in the same position sometimes for several days, but always outstretched. *C. foetidissimus* rested on the soil surface and in soil cavities as well as on rock faces. The Lysiopetaloidea can assume a tight protective spiral (Pl. 9, fig. 26) when disturbed, instead of running away (see Part 4, p. 324), but *C. foetidissimus* does not do this readily and instead it rapidly changes direction by running in a "hair-pin" bend. The animals were maintained in captivity for 11 months and appeared healthy when killed. They fed exclusively on animal food, taking mutilated spiders and opiliones etc., and locusts cut in half were their main diet. It seems unlikely that they can catch anything but small live prey, and they only took dead animals which were quite fresh. *Dischopetalum* laid eggs which hatched, but the young were not reared.

The function of the coxal sacs, which occur on legs 3 to 16 in Lysiopetaloidea and on most legs in *Polyzonium* (Part 4, p. 356), has hitherto been unknown. A *Callipus*, slightly desiccated by exposure to dry air and placed on blotting paper soaked in methylene blue, showed the blue colour in the coxal sacs after an hour's contact. All the sacs were then invaginated. It is probable that dew from rock faces can be absorbed by the coxal sacs in this way more quickly than would be possible by the mouth. An ability to drink dew may be very helpful for a rock-living habit in a hot mediterranean summer. The use of evaginated coxal sacs as adhesive organs was never observed in animals clinging upside down to rock faces, although evaginated sacs were sometimes seen. In *Polyzonium* an uptake of methylene blue could not be demonstrated, although it is possible that the very differently constructed coxal sacs of this animal may also serve for absorption of water as in Lysiopetaloidea, Symphyla (Tiegs, 1950), and certain Onychophora (*Opisthopatus*, Alexander & Ewer, (1955), see also Lawrence (1953).

Running.

The fleetness of these Lysiopetaloidea was at once apparent in the field. The maximum recorded speeds of *C. longobardius*, *C. foetidissimus* and *Dischopetalum* were 55, 52 and 35 mm. per sec. respectively, but much faster sprints have been observed. As in Chilopoda the Lysiopetaloidea run their fastest with reluctance. If the recorded speeds are scaled down* to a body size directly comparable with that of *Polymicrodon*,

* Speeds of Diplopoda and Geophilomorpha have been found to be roughly proportional to body length within the same species, and comparisons between different species are best made by taking similar diplosegment volumes in each (Part 2, p. 96).

a fast running nematophoran (see Part 4, Table II, p. 338), it is apparent that *Callipus longobardius* at 55 mm. per sec. runs almost twice as fast as *Polymicrodon*, although the leg lengths relative to diplosegment volumes in the two animals are about the same. This fleetness, although far exceeding that of any other millipede, is still much slower than a centipede. *Callipus* may achieve perhaps 80–100 mm. per sec., but a *Lithobius* or *Cryptops* possessing two segments of the same volume as a diplosegment of *Callipus* can exceed 200 mm. per sec., but only for a short time.

The general form of the legs and metachronal waves along the body in the Lysioptaloidea are very like those of *Polymicrodon*, compare Pl. 9, figs 24 and 28 with 23 and Part 4, Pls. 53–54, figs 18 and 28, the former in each showing about 5 propulsive legs followed by 9 recovering legs in a wave. The appearance of the legs during the forward stroke is similar, Pl. 9, figs 23, 30 and 33 showing the distal flexure raised raised high up the flanks, in contrast to most diplopods (figs 31 and 32). The larger number of diplosegments in the Lysioptaloidea allows six metachronal waves at a time instead of four as in fig. 23. The pattern of gait, expressed as the relative duration of forward and backward strokes, ranges from (5.0 : 5.0) to (7.0 : 3.0) when running freely, a gait of about (6.6 : 3.4) being most frequently seen in fast movement. Greatest speed is achieved with the coxae held close to the ground, as in Pl. 9, fig. 30, and with the footfalls close in, so that the tarsus is almost vertical when half-way through the back stroke (Pl. 9, figs 24 and 29). Slower running (Pl. 9, figs 28 and 33) results from the body being held further from the ground, with the use of a slower pattern of gait (8 legs instead of 5 in the propulsive groups marked by dots), the footfalls are further out, so that there is less apparent difference in the distance of the limb tips from the middle line when the claw is on and off the ground. As in other diplopods, the footfalls of successive metachronal waves may come close together; note the short black lines opposite the recovering legs in Pl. 9, fig. 25 and Part 4, Pls. 52–55, figs 11, 26 and 39. In fast running there is more dorsal humping of the body over the groups of recovering legs than is shown by *Polymicrodon* or *Cylindroiulus*, Part 4, Pls. 52 and 53, figs 10 and 18. This movement indicates a maximum backward and forward sliding of the sternites (Part 4, p. 339), and its more marked occurrence in the Lysioptaloidea is in keeping with their ability to take longer strides than all other diplopods.

Callipus can use as long a stride and as fast or faster a gait as can most centipedes (Table I, p. 495), but its pace duration is much longer, the minimum recorded figure being 0.3 sec. On a sprint the actual duration may be < 0.2 sec. in contrast to 0.07 by *Lithobius* and 0.04 by *Cryptops*.

Thus in comparison with other Diplopoda the Lysioptaloidea employ a short pace duration of the diplopodan order of magnitude, a slightly faster pattern of gait and a much larger angle of swing of the leg; and in comparison with Chilopoda they can show a faster pattern of gait than in the Anamorpha, a slightly larger angle of swing of the leg, but a longer pace duration (see Table I).

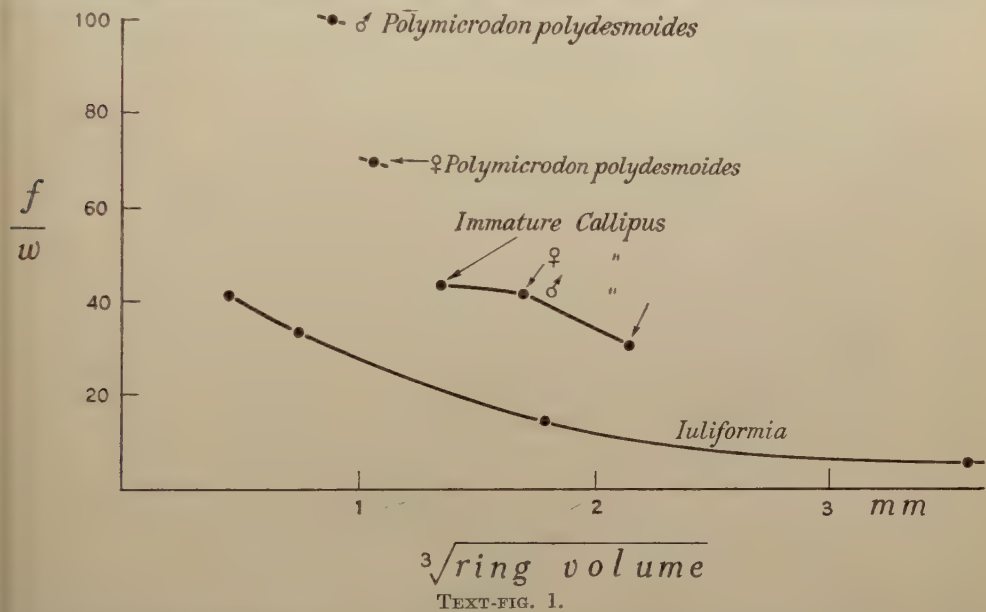
Pushing power.

An estimate of the pushing power has been obtained as described in Part 4, p. 302. *Callipus* and *Dischopetalum* are the only chilognath diplopods which have not readily pulled a sledge of weights to which they have been harnessed (the Pselaphognatha cannot be harnessed and they also do not push, Part 5). This reluctance to move against a resistance probably indicates that the Lysioptaloidea are not in the habit of pushing with the head end or the dorsal surface as other millipedes.

The size of a millipede affects the pushing force which it can exert, the force exerted by the legs, $\left(\frac{f}{w}\right)$, decreasing evenly with increase in size for a series of millipedes of approximately similar shape (Part 4, p. 343 and text-fig. 6, interrupted line). If the legs are relatively stouter, longer and stronger $\frac{f}{w}$ will be larger, and the

values for a series of such animals will lie on a curve further removed from the base line, see the points for *Tachypodoiulus* and *Plusioporus* on text-fig. 6, Part 4, the legs of *Plusioporus* being relatively longer than those of *Tachypodoiulus*.

The values of $\frac{f}{w}$ for the longer legged male and shorter legged female *Polymicrodon polydesmoides* of body lengths 15 and 17.5 mm. respectively, and for immature, female and male *Callipus foetidissimus* of body lengths 31, 38 and 52 mm. respectively are plotted against $3\sqrt{\text{diplosegment volume}}$ in text-fig. 1, together with the series of points for the smaller Iuliformia already shown on text-fig. 6, Part 4. The points for *Callipus* lie substantially nearer to the iuliform level than do those of either the male or female *Polymicrodon*, indicating that the leg movements of *Callipus* are weaker than those of *Polymicrodon* although leg lengths are comparable (Table. I p. 495). The points for *Dischopetalum illyricum* and the shorter legged *Callipus longobardius* lie respectively a little above and a little below the *C. foetidissimus* level.



TEXT-FIG. 1.

The force exerted by the legs ($\frac{f}{w}$) is plotted against the $3\sqrt{\text{diplosegment volume}}$ for *Polymicrodon polydesmoides*, *Callipus foetidissimus* and Iuliformia, showing that the leg movements of *Callipus* are weaker than those of *Polymicrodon*.

Callipus does not possess the sexual dimorphism in leg length seen in *Polymicrodon*. This dimorphism is also seen in *Polydesmus* (Part 4, Pl. 55, figs 28 and 29) and may be correlated with the litter living habit. The first three pairs of legs in *Callipus* are used in feeding in both sexes. Legs from the fourth pair backwards are ambulatory in the female but the male does not use the first ten pairs of legs (excluding gonopods) when running swiftly, although it may use them in slow movement; these stout legs lack the extra tarsal joint and are presumably used in copulation.

It is possible that the immobility of these legs results in a slightly higher $\frac{f}{w}$ for the female than the male *Callipus* in contrast to the much larger value for the male than the female *Polymicrodon*. The $\frac{f}{w}$ for *Microchordeuma* (Part 4, Table I, p. 332) is low

for the diplosegment size in comparison with other Nematophora because the legs are relatively shorter.

Thus comparison with other diplopods shows that the leg movements of the Lysiopetaloidea are weaker than those of litter living Chordeumoidea. Lysiopetaloidan fleetness is mainly due to an ability to move the leg quickly through a large angle of swing, an advance apparently made at the expense of the strength of the coxa-sternite articulation (p. 514).

Systematic position.

The special capacities of the Lysiopetaloidea are associated with their manner of life and morphology. Rock climbing scavengers may need to travel greater distances in search of food than herbivorous diplopods, and an abandonment of a conspicuous pushing habit has removed the need for leg strength.

The divided tarsal segment, which contributes to fleetness (p. 503) by facilitating flexure half-way through the backstroke, gives a vertical position to the extremity of the leg which also assists rock climbing by permitting easy convergence of the claws of paired legs (p. 503). The Lysiopetaloidea cling securely to rock faces at any angle (Part 4, p. 353), although they cannot negotiate glass-smooth surfaces as can the sucker-footed *Polyxenus*. The long body makes the crossing of rock crevices easier than it would be were the body as short as in *Polymicrodon*.

The suggestion was made in Part 4 that the long body of the Lysiopetaloidea might have been evolved in association with the burrowing in the iuliform manner, extra pushing force being obtained by the evolution of many diplosegments. The collum extends laterally as in Iuliformia, a feature perhaps associated with the ability to spiral tightly, but dorsally the head capsule arches above the level of the collum, as in Chordeumoidea, so that the collum cannot form a shield for head-on pushing. The evidence points to the absence of the iuliform type of pushing, and the present specialities are clearly fleetness, rock climbing and carnivorous feeding which have been perfected at the expense of leg strength. These are highly specialized habits departing widely from those of primitive diplopods. Carnivorous or scavenging feeding is practised to some extent by the Chordeumoidea. The exploitation of these habits is correlated with specializations of leg structure, the most marked being the coxa-body articulation (p. 511), the very mobile trochanter (p. 518), the divided tarsus (p. 503), the long extrinsic and intrinsic leg muscles (pp. 530 and 533), and the differentiation of many anterior legs for feeding and sexual purposes. Ample support is thus given for the view expressed in Part 4 that the Lysiopetaloidea do not represent a primitive group of diplopods. On the contrary they and the Pselaphognatha are the most highly specialized diplopods which have departed furthest from basic diplopodan habits and morphology (p. 545).

PRINCIPLES OF LEG DESIGN IN DIPLOPODA AND CHILOPODA.

The morphology of limbs is correlated with their manner of use and with their functions in Arthropoda as well as in vertebrates. To obtain an understanding of the limbs of terrestrial Arthropoda it is necessary to investigate different types of legs from many groups of animals ; from these details emerge the general principles governing leg design.

General features of limb movements and the functions which they perform.

The chilopodan leg typically executes movements resulting in speedy running (see Part 3) and the diplopodan leg exerts a greater force against the ground but gives less speed (Part 4). The geophilomorph centipedes are secondarily modified for burrowing and run more slowly than other Chilopoda (Part 3). Some Diplopoda (Polydesmoidea and Chordeumoidea) have secondarily become more fleet (Part 4) and the carnivorous Lysiopetaloidea have progressed further than all diplopods in the acquisition of fleetness by modifications of their basically diplopodan structure.

Greater modifications of limb movement and of common leg structure occur within the Diplopoda than in the Chilopoda, contrary to the statements of Verhoeff (1927). The Nematophora move their legs in a manner unlike that of the Iuliformia, Colobognatha, Oniscomorpha and Polydesmoidea, all of which show basic similarities. The legs of the Pselaphognatha, almost alone among diplopods, do not provide a pushing as well as a locomotory force and, their leg structure differs most widely from other diplopods (Parts 4 and 5 and p. 516). *Polyxenus* has achieved fleetness, as well as an ability to walk on smooth surfaces at any angle, by modifications of a diplopodan leg in a manner convergent with Chilopoda. The same fundamental type of leg structure and leg movement is shown by all Chilopoda, in spite of great superficial differences, such as those between the legs of *Scutigera* and the rest (Part 7).

Stride length.

An arthropod usually increases its speed by (1) quickening the pace, (2) employing a gait with a faster pattern (that is, one with a backstroke of shorter duration than the forward stroke) and (3) using a large angle of swing of the leg (Parts 2-4). The stride becomes longer at increased speeds, and its length depends upon the above factors, on leg length and on the nature of the coxal articulation with the body (see below).

In text-fig. 2 the tracks made by diplopods wearing a boot and running at or near their maximum recorded speeds are scaled to approximately the same diplosegment volume, so that their strides (distances between the black dots) are comparable. The strides of typically burrowing Iuliformia (figs *e* and *f* show a small and a large species) are much shorter than are those of the fleetier Polydesmoidea and Nematophora (figs *b*, *c* and *d*). *Tachypodoiulus niger* (fig. *a*) is relatively fleetest than the other two Iuliformia and its stride is longer. The stride of the fleet carnivorous millipede *Callipus longobardius* (fig. *d*) is remarkably longer than all the others.

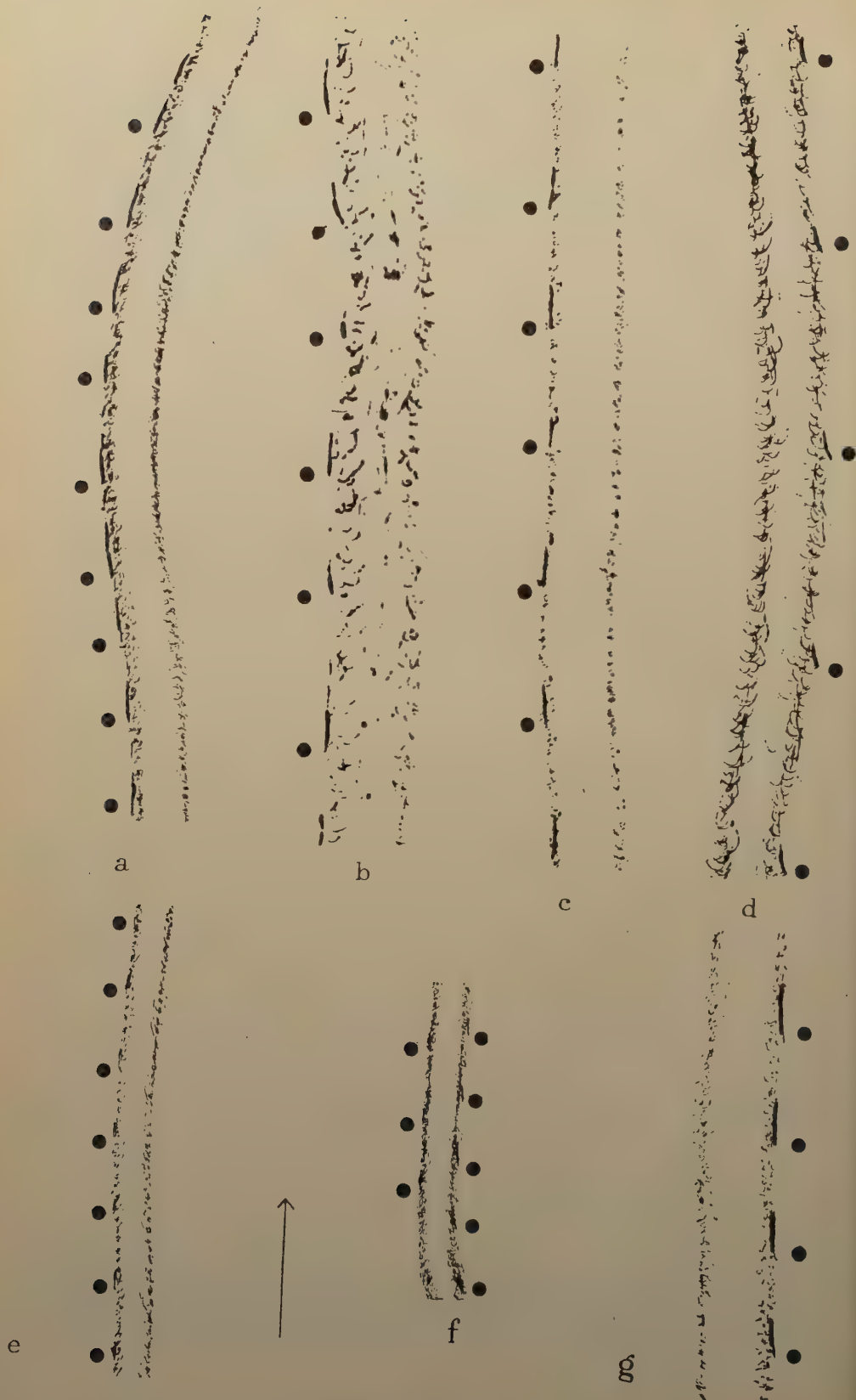
Table I, column 2 shows the stride lengths of millipedes and centipedes in a comparable manner. *Scutigera* and *Callipus* are the fleetest members of their groups and show the longest stride lengths; *Orya* and the last four diplopod entries are all slow moving, strong burrowers (although by different means) and show the shorter stride lengths.

The possession of longer legs may sometimes facilitate the execution of longer strides characteristic of the fleetier centipedes and millipedes (the Scolopendromorpha, Lithobiomorpha, Scutigeromorpha, Lysiopetaloidea and to a lesser extent the Chordeumoidea and Polydesmoidea), but comparison of columns 1 and 2 in Table I indicates that the manner of use of the leg (i.e. the gait, the angle of swing, etc) is the more important factor. The strides of the four millipedes with leg length 3.5 mm. range from 9 to 17 mm., and *Scutigera* with a leg $2\frac{1}{2}$ times as long as that of *Lithobius* takes a stride of less than $1\frac{1}{2}$ times that of the latter. Column 1 of Table I and text-figs 4, 5 and 6 show that except for *Scutigera*, the legs of Chilopoda are not longer than those of Diplopoda, about the same range of lengths being found in both groups, the apparent "legginess" of centipedes being an illusion due to the very different form of the body-segments.

A fast pattern of gait also contributes to stride length (see Part 3) and Table I, column 4, here shows that the long stride of *Callipus* is associated with a faster pattern of gait than occurs in any other diplopod and faster than that of any fleet chilopod except a scolopendromorph. (A fast pattern of gait is unusual in Geophilomorpha, and can only be executed slowly, see legend to Table I).

Angle of swing of the leg.

Angles of the swing of legs are difficult to measure with accuracy. An estimate of such angles, which is intended to show comparative values, is given in Table I, column 3. The figures are derived from a considerable number of photographs of animals taken in ventral view such as those shown on Pl. 9. The longer strides



TEXT-FIG. 2.

TABLE I

Animals scaled to common segment-volume	1 Leg length (in mm.)	2 Maximum stride length (in mm.)	3 Maximum apparent angle of swing of leg with claw on the ground	4 Fastest pattern of gait
CHILOPODA				
<i>Scutigera coleoptrata</i>	9	24	70°	6·4 : 3·6
<i>Lithobius forficatus</i>	3·5	17	85°	6·5 : 3·5
<i>Cormocephalus nitidus</i>	2·1	12	75°	8·9 : 1·1
<i>Cryptops anomalans</i>	2·3	10	75°	6·7 : 3·3
<i>Orya barbarica</i>	1·3	(7 and less)	85°	7·6 : 2·3
DIPLOPODA				
<i>Callipus longobardius</i>	3·5	17	90°	7·0 : 3·0
<i>Polymicrodon polydesmoides</i>	3·5	11	70°	6·5 : 3·5
<i>Polydesmus angustus</i>	3·5	10	75°	6·6 : 3·4
<i>Plusioporus sulcatus</i>	3·5	9	} 50°-65° }	6·1 : 3·9
<i>Tachypodoiulus niger</i>	3·1	8		6·2 : 3·8
<i>Cylindroiulus londinensis</i>	2·3	6		6·3 : 3·7
<i>Ophistreptus guineensis</i>	2·3	5		6·7 : 3·3
<i>Blaniulus guttulatus</i>	2·1	5		6·0 : 4·0
<i>Glomeris marginata</i>	2·8	3	40°	5·7 : 4·3

Table showing comparative leg lengths, maximum strides, angles of swing of the legs and fastest recorded patterns of gait of representative Diplopoda and Chilopoda. Dimensions of legs and strides are scaled to correspond with a common segment volume (diplosegment of Diplopoda or 2 segments of Chilopoda), that of a *Callipus longobardius* 5·8 cmm. Leg measurements refer to middle legs of the body, and apparent angles of swing are measured from coxal base to claw, when the claw is on the ground, from photographs taken in ventral view of animals running over cover glass. A further backward swing of the leg is effected by Chilopoda after the claw has been raised from the ground, see text. The stride and gait of *Orya* entered give the longest and fastest pattern respectively which have been recorded locally on the body during steady locomotion; most metachronal waves of movement show shorter strides and slower patterns of gait (see Part 3).

(The basis of the measurements of angles given in Part 4, p. 335, was not quite the same as that used here, and consequently the values are a little different.)

are associated with the larger angles of swing of the leg, and the swing of 90° by *Callipus* (Pl. 9, fig. 29) exceeds that of any centipede. The large entry for *Orya* is correlated with the shorter leg relative to segment length than is possessed by the Scolopendromorpha. *Dischopetalum illyricum*, running slowly (Pl. 9, fig. 28), uses a smaller angle of swing of the leg than that in fig. 29. The largest angle of swing of the leg recorded for *Tachypodoiulus* is shown in Pl. 9, fig. 27 for comparison with *Callipus*.

It is clear that for both millipedes and centipedes which run fast the ability to move the leg through a large angle and take a long stride are of importance, and that

TEXT-FIG. 2.

Tracks, made on smoked paper and printed in reverse, of millipedes wearing a boot. The black spots mark the footfalls of the booted legs. The tracks are scaled to a common diplosegment volume, and except for fig. "g" show the fastest speeds and longest strides which have been recorded on smoked paper. A forwardly directed mark is made by the boot as the leg is raised from the ground.

- (a) *Tachypodoiulus niger* . . . 26 mm. length.
- (b) *Polydesmus angustus* . . . 14 mm.
- (c) *Polymicrodon polydesmoides* . . . 15 mm.
- (d) *Callipus longobardius* . . . 42 mm.
- (e) *Cylindroiulus londinensis* . . . 26·5 mm.
- (f) *Ophistreptus guineensis* . . . 156 mm.
- (g) *Callipus longobardius* . . . 42 mm. running slowly.

these two assets are not required by millipedes and centipedes which are expert in burrowing. Maynard Smith & Savage (1956) have studied anatomical features of vertebrates illustrating the fact that muscles can be adapted either for rapid and weak or for slow and strong movement of the skeleton. They show, for example, that a contraction of one-fifth by the *teres major* muscle results in a rotation of the humerus of 50° in *Equus* and 30° in *Dasypus*. It will be seen that many functional problems facing the Arthropoda are shared in principle by the vertebrates, and that it is the manner of meeting these problems in the two groups which differ. The mode of use and the structure of arthropod legs serving the two opposed needs of weak and rapid or strong and slow movements of the body may now be considered.

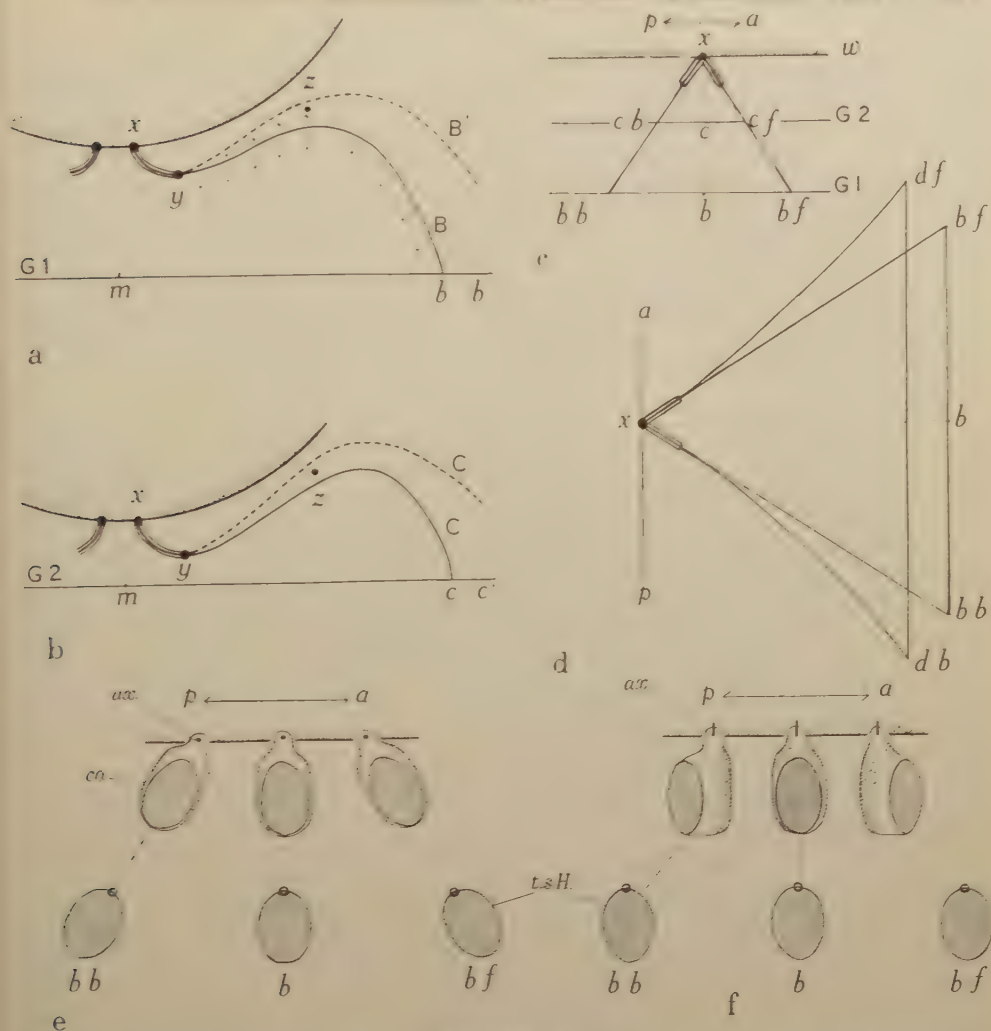
Basic modes of using a leg resulting in slow and strong or in rapid and weak movements.

The nature of the movement between the body and the coxa is various in the Arthropoda. It is well known that the majority of diplopods swing the leg backwards and forwards from a ventrally directed origin, no levator or depressor movements between coxa and body being possible; a similar movement is found on the thorax of decapod Crustacea. The axis of articulation in all these animals is roughly horizontal (see *ax* on Text-fig. 3e and p. 511). The legs of centipedes have a laterally directed origin; again no levator or depressor movements occur between coxa and body, and the axis of the forward and backward swing is roughly vertical. Some millipedes also have a vertical axis of swing of the coxa on the body in spite of a ventrally directed coxa (*ax* on text-fig. 3f and p. 511). When a leg arises ventro-laterally the axis of antero-posterior swing may lie obliquely in the transverse plane, as in the Symphyla. The legs of pterygote insects are very different, possessing sometimes a ball and socket joint between coxa and body which allows movement in all planes as well as rotation, as in the locust.

It will be shown how the two former types of coxal swing serve different needs, an approximately horizontal axis suiting strong pushing and an approximately vertical axis facilitating a long stride and therefore fleetness.

Leg utilization dependent upon an approximately horizontal axis of articulation between coxa and body, serving strong and slow movement (text-fig. 3e). The diagram in text-fig. 3a shows the typical stance of a iuliform millipede running freely, see Part 4, Pl. 52, figs. 9–11, with the leg (line *B*) flexed half-way through the backstroke. An S-shaped bend of the leg is necessitated by the mid-ventral origin of the legs (which gives cover for the legs when burrowing, see Parts 2 and 4 and below). Text-fig. 3c shows the same leg but in side view, the lines *x-bf* and *x-bb* indicating its position at the beginning and end of the backstroke when the limb is fairly straight, the distance between the body wall *w* and the ground *G1* being the same in the two figures. The distance *bf-bb* equals the distance the leg base and body travel during the propulsive backstroke; the stride, other factors being equal, is proportional to this distance (Part 1). Now if the two flexures of the S-shaped bend of the leg become more acute (line *C* in text-fig. 3b), the ventral surface of the body will lie closer to the ground (*G2* in text-fig. 3b and c) and if the leg swings through the same angle, the line *bf-bb* becomes reduced to *cf-cb*.

The power of the musculature of a limb may be taken as constant for any one animal. Since power can be expressed in terms of force, distance and time, it follows that more force can be exerted against the ground in the stance shown in text-fig. 3b than in fig. 3a, a reduction of the distance *bf-bb* to *cf-cb* allowing a corresponding increase in the force, while the pattern of gait, the pace duration and angle of swing of the leg remain the same. Iuliform millipedes running as fast as they can for escape might be expected to show the stance of text-fig. 3a and when pushing to show the stance of text-fig. 3b. This indeed is the case, contrast figs 9, 10, 11 and 15 with figs 12, 13, 14 and 16, Part 4, Pls 52–53. "Getting down to it" appears to be a neat way of "going into bottom gear" by reducing the stride length.



TEXT-FIG. 3.

Diagrams showing basic movements of diploped legs, and the effect upon the stride of different type of stance and coxal sternite articulation. The leg length in all diagrams is that seen in text-fig. 4a. The coxa swings backwards and forwards about a horizontal axis in fig. c and in fig. d about a vertical axis and through the same angle as in fig. c.

- (a) View from transverse plane of a iuliform leg half-way through the backstroke with the body held well off the ground, as in fast running.
- (b) Similar view of same leg with the body held close to the ground, as in pushing and burrowing.
- (c) Lateral foreshortened view of the leg shown in figs a and b, but at the beginning and end of the backstroke, the ground being at the levels G1 and G2.
- (d) Dorsal view of a leg of similar length, at the beginning and end of the backstroke, but moved through a horizontal coxal swing (as in Nematophora). The effects of horizontal bending of the leg are shown by the lines X-df and X-db.
- (e) Diagrammatic lateral views of a ventrally directed coxa swinging 30° forwards and 30° backwards about a horizontal axis ax in the transverse plane of the body. The distal part of the leg is cut off. Below each coxa sections of the leg, transversely through a hinge joint (H.1.-H.3. on text-fig. 4a right side), are drawn relative to the ground to show the corresponding forward and backward rotation of the dorsal hinge, marked by a ring.
- (f) Diagrammatic lateral views of a ventrally directed coxa swinging about a vertical axis ax . The distal part of the leg is cut off. Below each coxa sections of the leg, transversely through a hinge joint, are drawn relative to the ground to show the absence of any displacement of the dorsal hinge, cf. fig. e. (No diploped coxa swings exactly about either a horizontal or a vertical axis, see p. 509.)

For further description see text.

The practicability of these two types of stance is limited. If the pushing stance is carried to extremes by the leg flexures being great enough to bring the limb tip nearer to the horizontal level of the fulcrum x than in text-fig. 3*b* and *c*, a very small stride or none at all will result from the same coxal swing. If on the other hand the animal stands higher from the ground, the line $bf-bb$ can be lengthened, using the same angle of swing of the leg, only if the outstretched leg at the beginning and end of the backstroke can still reach the ground. Placing the claw on the ground nearer to the middle line of the track will facilitate the execution of such a pace, but will increase the necessary flexures of the leg when half-way through the backstroke. Tracks made by millipedes running at maximum speeds are slightly narrower than those made when running slowly. The tracks of *Callipus* shown in text-fig. 2*g* and *d* show this contrast, and indicate that millipedes do in fact make such adjustments.

Leg utilization dependent upon an approximately vertical axis of articulation between coxa and body, serving weak and rapid movement (text-fig. 3f). The diagram in text-fig. 3*d* shows a dorsal view of a leg of the same length as that in the other figures. It swings through the same angle as in fig. 3*c*, but the axis of swing is vertical (as in text-fig. 3*f*) and the body is near the ground. The leg is almost fully stretched at the beginning and end of the backstroke, $x-bf$ and $x-bb$, and half-way through the backstroke the leg is flexed along the line $x-b$. The line $bf-bb$ in fig. 3*d* is nearly twice as long as it is in fig. 3*c*, although the coxa swings through similar angles in the two cases. The lines $x-df$ and $x-db$ show the effect of bending the leg distal to the coxa in the horizontal plane. The claw can then reach further forward, but must be placed on the ground nearer to the middle line. A slight curvature of the leg first forward and then backward makes the distance $df-db$ nearly three times as great as the distance $bf-bb$ in fig. *c*.

It is clear that the movements shown by text-fig. 3*d*, which give about twice the stride length of those in fig. 3*c* while using the same angle of swing, are the more suitable to animals requiring speed. A coxa swinging about a vertical axis (text-fig. 3*f*) will supply a leg which will not give a strong pull but which will carry the small weight of the animal forward with much greater speed than will a coxa swinging horizontally as in text-figs 3*a*, *c* and *e*. Centipedes and also the Nematophora, Pselaphognatha and Polydesmoidea swing their legs about an approximately vertical axis; the Polydesmoidea can also exert a strong thrust with their very robust legs. Table II, Part 4, p. 338 and Part 5 show that these are the fleetest dipodops.

When the coxa swings about a vertical axis, the longer strides will be obtained when the body is carried close to the ground, because a leg cannot reach so far forward and backward when the body is far from the ground. *Polymicrodon* and the Lysio-petaloidea, Pl. 9, figs 23, 30 and 33, show the former stance, the coxae just clear the substratum, in contrast to the short and long-legged Iuliformia running fast, figs 31 and 32, where the longest strides are obtained when the coxae are high off the ground. The longest strides will be obtained when the footfalls lie nearest to the middle line (see above and text-fig. 2*d* in contrast to 2*g*), the stride length will be $db-df$ instead of $bb-bf$ on text-fig 3*d*, the leg flexing considerably when half-way through the backstroke, any slight promotor and remotor movements of the distal leg segments at the beginning and end of the backstroke respectively increasing the stride and speed.

General features of limb musculature of Diplopoda and Chilopoda.

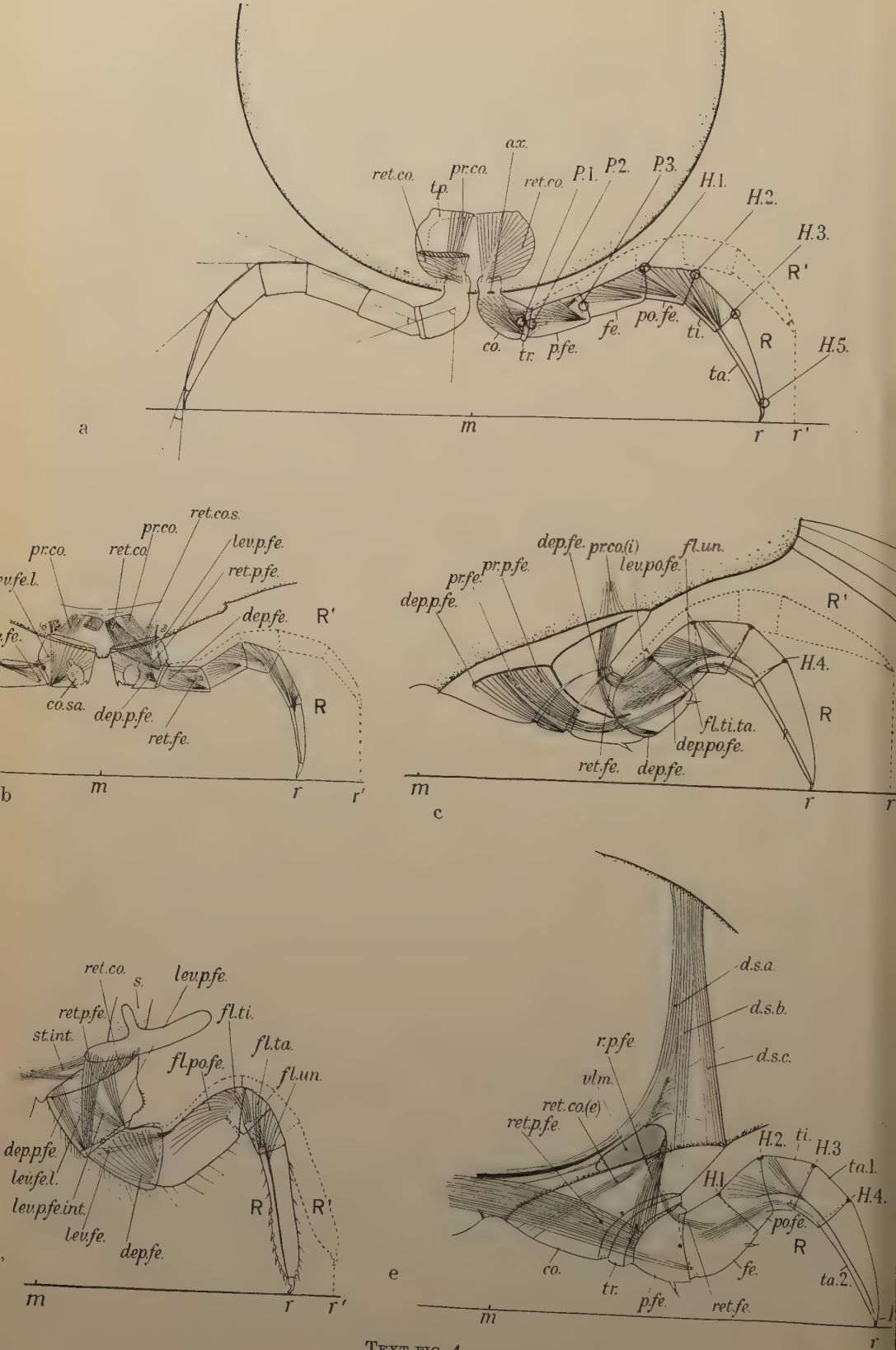
Similar extrinsic muscles contracting by the same amount in the same time could give either slow strong leg movements when the axis of coxa-body articulation is horizontal or faster weaker movements when this axis is vertical (p. 496). Speciali-

zation of the coxa-body joint resulting in a larger angle of swing for the same muscular displacement will further increase the speed. The Lysiopetaloidea have evolved such a joint (p. 514). Intrinsic protractor and retractor muscles, if they cause actual bending of the leg, may elongate the stride still more. Any enlargement of the T.S. area of an extrinsic retractor muscle will increase the tension which it can generate, while a linear extension of the muscle will increase the displacement which is caused by the same degree of contraction. Animals exhibiting a strong pushing ability might be expected to possess wide extrinsic retractors and those needing fleetness might benefit by the possession of long extrinsic muscles. A longer extrinsic muscle will undergo less deformation in giving the same displacement at one end than a shorter muscle, and length may thereby contribute to efficiency, since this is maximal when tension is developed isometrically. The length of an extrinsic muscle must also be related to that of the leg, the lever action of a longer leg needing a corresponding increase in the extrinsic retractors if a similar force is to be exerted on the ground by the claw (see also p. 547).

No series of diplopods and chilopods can be subjected to a simple direct analysis because of their complexity, but they bear out the general applicability of these principles. Burrowing Diplopoda show the maximum width of extrinsic retractors. Longer narrower retractors are found in the fleetier diplopods and chilopods. If, leg length be taken as unity the lengths of the extrinsic retractors in strongly pushing Iuliformia is about 0.15, those of the fleetier *Polydesmus*, *Polymicrodon* and *Callipus* are 0.2, 0.22 and 0.25, the fleetness of these animals increasing in the same sequence, and 0.37, 0.67 and 0.62 for *Lithobius*, *Scolopendra* and *Polyxenus*, the Chilopoda being fleetier than all Diplopoda and *Polyxenus* using a very large angle of swing and rapid stepping for a diplopod. Exceptionally short-legged Iuliformia (*Poratophilus*) or long-legged Chilopoda (*Scutigera*) have values rather opposite from the above because tracheal pouches which carry the extrinsic leg muscles serve other needs besides providing apodemes, and do not decrease in length proportionately with the legs, and the trunk of *Scutigera* has no space for extrinsic muscles of lengths proportional to that of its legs. *Scutigera* also is content with much smaller displacements at the coxa-body articulation.

Intrinsic leg muscles will be expected to differ in strong burrowers and in fleet runners. Many short muscles will provide strength all along the leg in burrowers. Fleetness by a long stride leads to greater flexure of the leg when half-way through the backstroke, skeletal features facilitating the bends, and a larger range of joint displacements occurs in fast runners than in burrowers (p. 503). Longer muscles might be expected to be present in the legs of fast runners and short muscles and many of them in the legs of strong burrowers. Long intrinsic muscles are conspicuous in *Polyxenus*, *Nematophora* and Chilopoda. The legs of the Lysiopetaloidea possess a flexor tarsi longus extending to the anterior edge of the trochanter, resembling in principle the long flexor unguiculi also reaching to the trochanter of centipedes (except *Scutigera*), compare text-fig. 5g with 6. Long levators are present in these animals only. The strong pushers, on the contrary, show short flexors and levators, text-figs 4a, 5h, 17a and b, p. 532.

Long muscles possibly serve another need in fast runners. Fast muscles of similar structure but of different lengths probably are capable of full contraction in the same time. An absolute displacement at a joint may be effected more quickly by a long muscle than by a short one, leg lengths remaining the same, since a fixed displacement represents a smaller proportion of the total potential shortening of the long than the short muscle. It is seldom possible to show increased speed of movement occurring independently from increased displacement because the two phenomena usually accompany each other, but selected Geophilomorpha and Scolopendromorpha provide an example. The nature of the gait and body shape fix a similar upper limit to the angle of swing of the leg in both groups, and the Scolopendromorpha step much more quickly than the Geophilomorpha. The plan of limb musculature



TEXT-FIG. 4.

is similar in the two, but if leg length in each be taken as unity, the length for example of the retractor trochanteris to the sternite (*ret.tr.s.* in Part 7) is 0.67 in the Scolopendromorpha and 0.5 in Geophilomorpha (*Orya barbarica*), suggesting that the longer muscles of the former may facilitate their speed. In *Lithobius* these muscles cross over to the opposite side of the sternite as in the Scolopendromorpha, and are as long as is mechanically possible, but the extra length of leg now results in slower stepping, although similar body speeds are obtained in consequence of the longer stride (see also p. 547).

Since the power of a muscle can be expressed in terms of force, distance and time, the swifter the stepping and the longer the stride the smaller will be the force exerted by the muscle. The weakness of extrinsic muscles providing swift movements is compensated for by an increase in their number. Most Diplopoda possess only 2 extrinsic muscles, the fleeter Polydesmoidea and Nematophora 4 and 5 respectively, while the number increases in the Chilopoda to 13, 18, 20 and 33 in Geophilomorpha, Scolopendromorpha, Lithobiomorpha and Scutigleromorpha respectively, the very large number in the latter being correlated with extremely long legs in these small animals.

Leg positions and flexures.

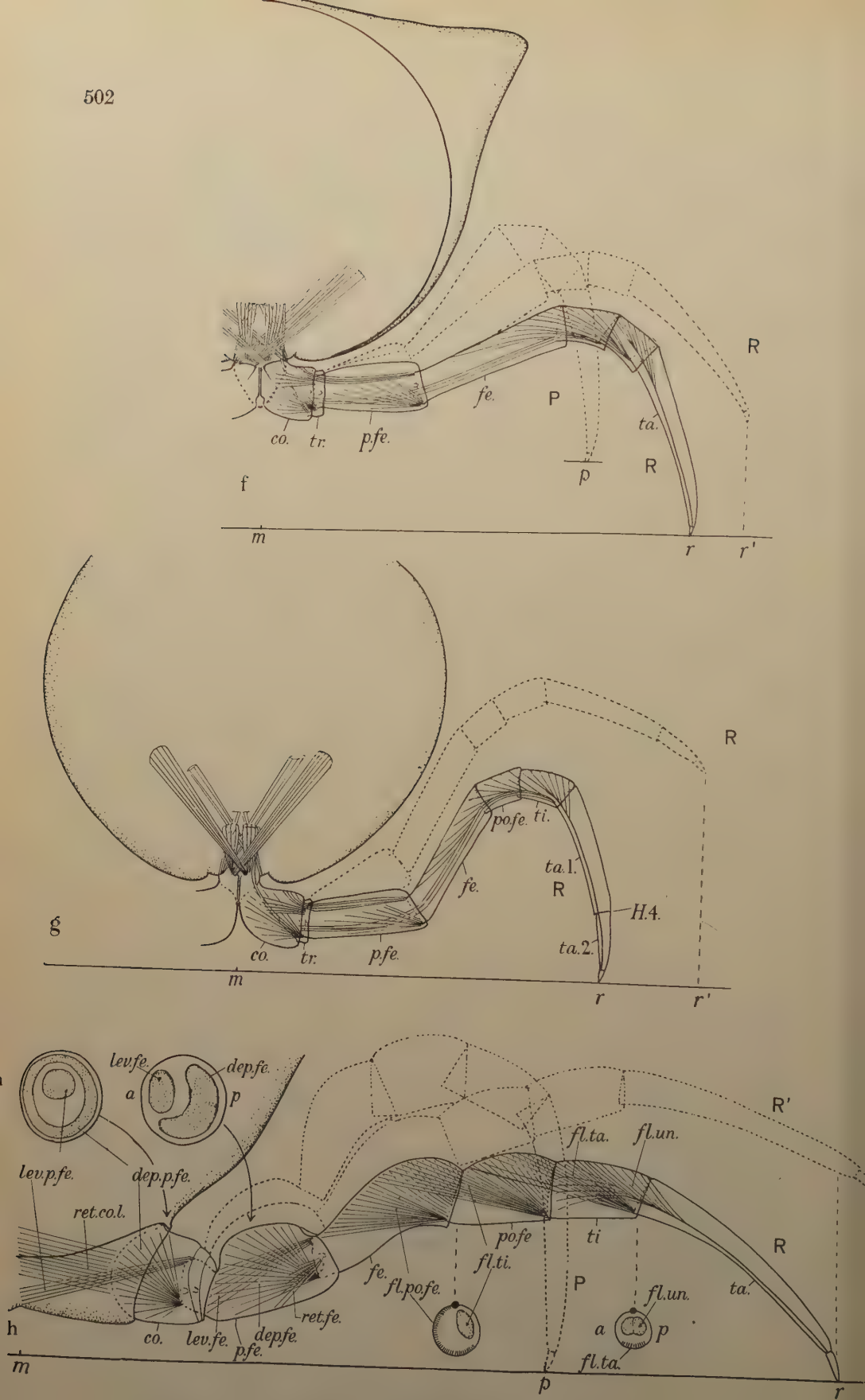
In text-figs 4-6 diagrams of diplopods and chilopods, based upon photographs and scaled to a common segment volume, show the normal stance when running on a smooth surface, the legs *R* being half-way through the backstroke. Leg lengths are roughly comparable, and an indication is given of the principal muscles and types of joints, details of both being shown on text-figs 7-21. The movable parts of the leg in Iuliformia, Oniscomorpha, Colobognatha and Nematophora, text-figs 4*a*, *b*, *d* and 5*g*, show the S-shaped bend referred to above, which is necessitated by the ventral origin of the legs (Part 4), and the need either to exert a strong thrust on the ground or to use a long stride (p. 498). The proximal component of this bend is absent in the Polydesmoidea and Chilopoda, and is much compressed in the Pselaphognatha, which have little coxal mobility, because the more lateral origin of the leg (or of its most movable part in the Pselaphognatha) eliminates any need for such a bend.

The Iuliformia can readily accentuate this S-shaped flexure, but the Colobognatha and Oniscomorpha do not, and when pushing their bodies are not brought so close

TEXT-FIG. 4.

The diagrams in text-figs 4-6 show the normal stance when the legs are half-way through the backstroke in the main orders of Diplopoda and in Lithobiomorpha and Geophilomorpha, drawn to an approximately common diplosegment volume, so that leg lengths are directly comparable. The legs are shown in posterior view except in figs *c*, *i* and *k*. The limb musculature of the Iuliformia, Nematophora and Chilopoda is incomplete; for details see text-figs 17-21 and Part 7. *R* shows the legs half-way through the propulsive backstroke when running freely, and *R'* the corresponding position in the recovery forward stroke. *P* shows the leg when pushing with the dorsal surface or resting.

- (*a*) A iuliform millipede. On the right are shown the positions of the pivot joints *P.1-P.3* and hinge joints *H.1-H.5*, and on the left the angular displacements at the joints and the bend of the coxa are indicated.
- (*b*) A colobognathan, *Polyzonium germanicum*, levator prefemoris is drawn on the left side only; it lies anterior to depressor prefemoris.
- (*c*) A pselaphognathan, *Polyxenus lagurus*, anterior view.
- (*d*) An oniscomorph, *Sphaerotherium giganteum*, all leg muscles are shown.
- (*e*) Posterior view of limb musculature of *Polyxenus lagurus* showing muscles not clearly drawn in text-fig. 4*c*, or in Part 5, text-fig. 3, for comparison with chilopod muscles shown in text-figs. 6*i* and *k* and in Part 7. Three black dots show the levels of pivot joints on anterior face of leg.



TEXT-FIG. 5.

to the ground (Part 4, Pls 54–55, figs 29, 30, 48 and 49) and the Colobognatha and Oniscomorpha are feeble pushers than the Iuliformia (Part 4, Table I, column 9). The angular contributions to the S-shaped bend by different parts of the leg are indicated on the left of text-fig. 4a. The curvature of the coxa itself provides a 60° upward bend followed by a considerable lift at the trochanter-prefemur joint and a smaller lift at the prefemur-femur joint. The more distal joints effect the downward flexure. The great curvature of the iuliform coxa, which brings the distal part of the trochanter more nearly into the vertical plane than does that of the Colobognatha and Oniscomorpha (compare text-fig. 4a with *b* and *d*) appears to be a specialization contributing to strong pushing since it accentuates the S-shaped bend (p. 496).

An acute curvature of the nematophoran coxa through about 90° brings the distal end of the trochanter into a vertical position also (text-fig. 5*f* and *g*) but here this is associated with the needs of speed. The vertical axis of coxal articulation with the body is neither robust nor suited to strong pushing by the head (p. 514), and the leg needs to swing out as close to the body as possible, so giving a maximum stride. It will be shown in a subsequent Part that the Symphyla are not concerned either with pushing or with speed, and they lack an acute proximal upward bend to their legs.

The dotted lines *R'* in text-figs 4–5 show the positions of the legs when half-way through the forward stroke as accurately as can be judged from measurements and from photographs such as those on Pl. 9 and Part 4, Pls 54–55, figs 22, 28, 38–41 and 48. The points *r* and *r'* are further apart relative to the distance *r–m* in *Polyzonium*, *Polyxenus* and *Callipus* than in the others. This means that the leg is considerably flexed in position *R*. Such flexure brings the tarsus to a more vertical position than in text-figs 4a and 5*h*, facilitating a converging grip by paired claws in climbers such as *Callipus*, *Polyzonium* and *Polyxenus* (Parts 4 and 5). The ability to flex the leg acutely in position *R* also facilitates a long stride with a large angle of swing as in *Polyxenus*, *Callipus* and fast running Scolopendromorpha and Lithobiomorpha. An additional joint across the tarsus, *H.4.* in text-figs 4*e*, 5*g* and 6*k*, will assist this acute flexure, and it may be suggested that this joint has been evolved in a parallel manner in Diplopoda and Chilopoda in association with fast running.

Many animals show a divided tarsus on the posterior legs only: for example legs 7–18 in *Cryptops spinipes* have an incomplete division while legs 20 and 21 possess a complete joint; *Lithobius duboscqui* lacks a division on legs 1–10; the terminal legs alone in *Craterostigmus tasmanianus* have a divided tarsus, and all walking legs except 1–3 in the female and 1–10 in the male *Callipus foetidissimus* have this division. The tendency to divide the tarsus appears to be associated initially with increase in leg length and fleetness. Legs 1–14 of *Craterostigmus* are shorter than those of *Lithobius forficatus* or *L. variegatus* and *Craterostigmus* runs slowly. The three anterior legs of *Callipus* are shorter than the rest in both sexes and show modifications for use when feeding, while legs 4–10 in the male differ markedly from the rest and may be used for holding the female. Slow stepping can be carried out by all anterior legs in both sexes, but legs 1–3 in the female and 1–10 in the male are not used in fast running.

The tarsus of the Oniscomorpha is also held steeply (text-fig. 4*d*), but the angle of swing of the leg is small and the leg unflexes but little on the forward stroke, the movement being restricted by the wings of the tergites. The claw is not raised far

TEXT-FIG. 5.

Limbs (cont.).

(*f*) A nematophoran *Polymicrodon polydesmoides* female.

(*g*) A nematophoran *Callipus longobardius* female.

(*h*) A polydesmoidean *Polydesmus angustus* male, with diagrammatic transverse sections through the coxa and prefemur and across the proximal ends of postfemur and tibia at the levels indicated. All muscles are shown.

off the ground and therefore a semi-permanent and extreme flexure can be maintained at the femur-postfemur joint, and no extra tarsal joint is needed.

The dotted lines *P* in text-figs 5*f* and *h* show the probable position of the leg when *Polymicrodon* and *Polydesmus* are pushing with the dorsal surface among layered leaves etc. Legs at rest are often brought into this position close under the keels. A straightening of the proximal bend of the leg and a relaxation of distal flexors will raise the body. The tarsus is almost vertical. For such a movement another joint across the tarsus would be unsuitable; if it were present it would need to be rigid at the moment when the tergum is raised and the distal flexor muscles of the leg relax, and only blood pressure could make it so. Such a leg would be weakened for pushing with the dorsal surface. Thus it is suitable for *Polydesmus* and *Polymicrodon*, both fairly fleet millipedes, to have an undivided tarsus since they live among woodland litter, in contrast to the *Lysiopetaloidea*, much fleetier millipedes living in rocky places, which benefit by the possession of this joint. In photographs *Polymicrodon* frequently runs as in text-fig. 5*f* with the body well off the ground, although it can run with the coxae close to the ground as in Pl. 9, fig. 23, a stance giving the greatest stride. This stance is usual in the *Lysiopetaloidea* where the divided tarsus may facilitate the movement. Over rough ground *Polydesmus* stands up more than in text-fig. 5*h*, the footfalls occurring between points *r* and *p*, and the stride is less.

The *Pselaphognatha* and *Polydesmoidea* show two different methods of secondary elimination of the initial part of the S-shaped bend. The dilatations on the pedigerous lamina of the latter bring the proximal rim of the coxa to an almost lateral position, and the bun-shaped relatively immobile coxa of *Polyxenus* brings the mobile prefemur to a similar position, superficially resembling the insertion of the legs of *Chilopoda* (text-figs 4*c*, *e*, 5*h*, 6*i* and *k*). The swing of the leg in all takes place about an axis approaching the vertical, so facilitating long strides and fast running.

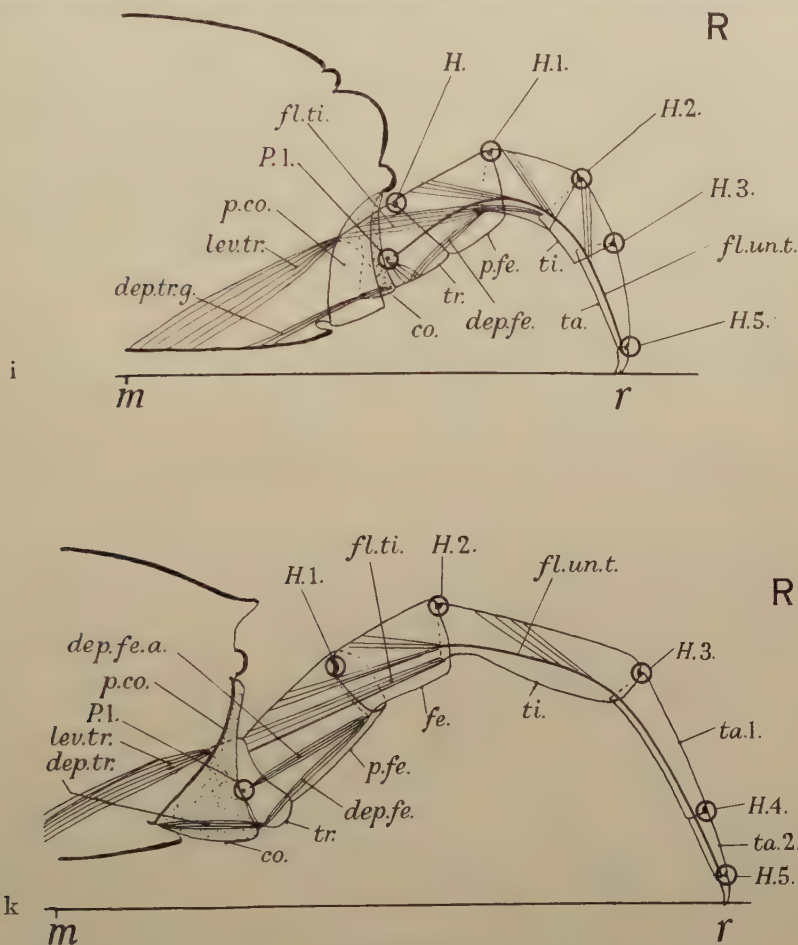
Types of leg joints and their distribution.

Three factors govern the morphology of joints: (a) The plane or planes of the required movement, (b) the necessary strength of the joint, and (c) an economy of muscles operating the joint is advantageous. A ball and socket joint gives obvious advantages in its variety of movement, but flexure in one plane requires muscles to prevent movement in others. Ball and socket-like joints are rare in arthropods; they occur for example between the diplosegments of diplopods and between coxa and body in some insects. If skeleton instead of muscles is employed to prevent movement in some planes, an economy in muscles results. The leg joints of diplopods show a maximal use of skeleton to control movement, thus making the greatest amount of muscle available for direct locomotory purposes.

There are three main categories of leg joints, (1) between the coxa and the body giving movement in various fixed planes which always differ from those of the succeeding leg joints; (2) pivot joints, in which the axis of movement passes horizontally through the middle of the overlapping leg segments, shown by circles on the anterior or posterior faces of the leg *P.1.-P.3.* in text-figs 4-6*a*, *i* and *k* and (3) hinge joints situated dorsally at the junction of the leg segments, shown by dorsal circles *H-H.5.* on the figures. Joint (1) swings the whole leg forwards and backwards, and is operated by extrinsic muscles. Pivot joints allow both levator and depressor muscles to act as antagonistic pairs, and hinge joints normally are flexed by muscles and extended during stepping by the movement due to extrinsic retractors, and when off the ground by blood pressure, there being no elastic cuticle at the joints capable of extending the leg when the flexor muscles relax (see also p. 524).

Diplopoda possess at most three pivot joints while *Chilopoda* possess only one, that between coxa and trochanter. Diplopod pivot joints are mechanically strong, suiting the forceful thrust exerted on the ground (516). The chilopod pivot joint

superficially appears unlike those of diplopods, but it is in fact based on the same plan, which is modified to give a wider range of movement than is possible for a simple strong pivot joint, but the resulting joint is too weak to transmit a large thrust. This anterior and very mobile pivot joint of Chilopoda suited to fast running occurs by convergence in the *Pselaphognatha* also. If a leg is to be strong several pivot



TEXT-FIG. 6.

Limbs (cont.).

(i) The geophilomorph centipede *Orya barbarica*, anterior view with coxa stippled.

(k) The lithobiomorph centipede *Lithobius forficatus*, anterior view with coxa stippled.

The scale in both figures is comparable with those of text-figs 4 and 5, two segments of a chilopod being taken as equal to a diplosegment of a diplopod.

joints, each with a smaller range of movement, are the more appropriate as are found in most Diplopoda.

The ventral origin of the legs in diplopods makes it impossible for levator movements to be concentrated near the base of the leg. The chilopod leg can effect a major upward swing at the coxa-trochanter joint, but in diplopods, other than Polydesmoidea and Pselaphognatha, this is not possible owing to the overhang of the body, and two or three pivot joints are needed. Text-fig. 3a shows a typical diplopod, the coxa $x-y$ swings antero-posteriorly, from y to z levator and depressor muscles

exert upward and downward forces, while from z to the claw flexor muscles alone operate.

Four or five hinge joints lie distal to the pivot joints in Diplopoda and Chilopoda. These hinges correspond with the series of leg segments in Diplopoda, four being the usual number, and a fifth is added by division of the tarsus in the Pselaphognatha and Lysipetaloidea (see above). A typical dorsal hinge is present between trochanter and prefemur in the Geophilomorpha, but in other Chilopoda this joint is not movable and no hinge is present (text-fig. 6*i* and *k*).

The single pivot joint of the Chilopoda enables the leg to function with a minimum of levator muscles and a maximum of propulsive intrinsic flexor muscles. The levator muscles need to be long to give sufficient displacement, but they are not needed beyond the single pivot joint and can therefore be extrinsic in position thus taking up very little leg space. Such a leg is not robust, its segments are easily displaced, as can be ascertained on a narcotized chilopod, the leg is unsuitable for the requirements of burrowing Diplopoda, but is eminently fitted for transmitting a small force rapidly as needed by fleet chilopods.

Sizes and shapes of leg segments.

The lengths and shapes of leg segments are correlated with the various functions of the legs, with the stance and with the needs of muscles. Verhoeff (1903) classified limb musculature into (*a*) direct muscles, crossing one joint only and (*b*) indirect muscles crossing more than one joint. A very short segment can only house short direct muscles, and these in turn can only effect a small distal displacement at the joint.

The diplopod coxa is probably as short as is mechanically suitable if it is to house a bulk of intrinsic muscle capable of levating and depressing the whole distal part of the leg. The Chilopoda need longer levator muscles which will effect a greater displacement of the single pivot joint; extrinsic muscles serve this need in a manner mechanically impossible to most Diplopoda, and consequently the coxa can be very short indeed. A short coxa makes the trochanter and prefemur the more accessible to extrinsic muscles, and brings the pivot joint close in so that levation may take place near the body. The Polydesmoidea have a shorter coxa than the Iuliformia, resulting in the chilopodan type of mechanical advantage, the lateral origin of the coxa allowing levator muscles to be extrinsic.

In both Diplopoda and Chilopoda which burrow, the segments of the leg tend to be short and wide and, except for the trochanter, not very different from one another in length (text-figs 4*a* and 6*i*). In the faster runners of both groups the legs are longer, the major increases being situated in the prefemur, femur and tarsus in Diplopoda and in the tibia and tarsus in Chilopoda. The maintenance of a short coxa, trochanter, postfemur and tibia in diplopods (text-figs 4-5, *e*, *g* and *h*) enables the basic leg flexures to be concentrated in position, so allowing the acute bends seen in *R*, text-fig. 5*g* and *P*, figs 5*f* and *h*. The Chilopoda on the other hand use the free upward flexure at the proximal pivot joint and the downward bend at the femur-tibia joint as the principal contributing factors to leg flexure; their legs project laterally, but no disadvantage is attached to this except in the Geophilomorpha, and here the legs are very short, much shorter relative to segment volume than in most Diplopoda (text-figs 4-6 and Part 4, Table I, p. 332).

In the fleetier Diplopoda and Chilopoda the distal elongation of the leg results in long thin terminal segments possessing tendons and little muscle, the bulk of the muscle lying proximally as in ungulates. This lightening of the extremities doubtless facilitates rapid extension of the leg.

The functional evolution of the trochanter. The trochanter in myriapods has been identified as a true leg segment, as a "complementary ring" and as a segment part-

ially cut off from the coxa or prefemur. Verhoeff (1903) believed that a leg with fewest segments was the most primitive, and that the trochanter to-day can be seen in process of separation from other leg segments in various myriapods. Börner (1903) showed the inaccuracy of Verhoeff's statement that a trochanter had no muscles of its own. The present study suggests that a free trochanter differing little from other leg segments in size and possessing its own direct and indirect muscles is the more primitive condition among living forms, such a trochanter is seen in the Geophilomorpha: that the most primitive diplopod trochanters are slightly movable and occur in the Colobognatha and smaller Iuliformia (text-figs. 4*b* and 9*a-b*); and that the trochanter has become shorter and fused either with the prefemur or with the coxa, or has become specially mobile, in meeting functional requirements of the several orders of Diplopoda and Chilopoda, direct muscles having disappeared as the trochanter became shorter (p. 518).

Levator muscles in diplopod legs are intrinsic, with the exception of the Polydesmoidea, owing to the position of origin of the coxa. The diplopod trochanter is always much shorter than either the coxa or the prefemur, and two sets of levator and depressor muscles serve the three pivot joints. These muscles are longer than they would be if the coxa, trochanter and prefemur were equal in length and housed their own direct muscles. It is probable that a short trochanter may have been acquired by ancestral Diplopoda in association with the need to obtain long muscles giving sufficient displacement for an acute proximal bend of the leg.

A perfection of pivot joints *P2* and *P3* (text-fig. 4) in Iuliformia and Oniscomorpha combines strength with mobility, and in larger Iuliformia the leg is further strengthened by partial fusion of the trochanter with the coxa, so losing one pivot joint. This fusion is complete in the Oniscomorpha where the leg unflexes but little and the range of proximal leg bending is small (text-fig. 4*d*). The most mobile trochanters in Diplopoda are possessed by Polydesmoidea and Nematophora where long strides from long legs need considerable range of proximal leg flexures, compare text-figs 4*a*, *b* and *d* with 5*g* and *h* (pp. 518 and 535). Morphological specializations permitting these movements are described below.

The absence of mobility at the junction of trochanter and prefemur in the three swiftly moving orders of Chilopoda (Scolopendromorpha, Lithobiomorpha and Scutigermorpha) is associated with the problem of effecting adequate and rapid levation of a leg of increasing length from one pivot joint (text-fig. 6*i* and *k*). Longer distal segments result in the femur becoming horizontal or forming part of the upward instead of the downward bend of the leg. Levator muscles pull on the trochanter alone, and if this segment is short and fused with the prefemur, both will easily levate together. The nature of the trochanter-prefemur fusion (see text-fig. 11*b*) suggests that the trochanter may act also as a spring during rapid locomotion (see p. 522).

Distal and proximal ends of leg segments. The shapes of the proximal and distal ends of leg segments are also correlated with function. Nearly all segments show a thick proximal margin set at right angles to the long axis (text-figs 9, 10, 13, 14, 15, 19, and 20) from which muscles pass proximally. The chilopod trochanter is an exception (see text-fig. 11*b* and p. 520). The proximal end of the prefemur in the Colobognatha and Oniscomorpha is emarginated dorsally, so compensating for the lack of curvature of the coxa and assisting the initial upward bend of the leg (text-fig. 4*b* and *d*). Emarginations of the distal end of a segment all increase the ease of flexure towards the emargination. The prefemur often shows a distal dorsal emargination which assists the proximal upward bend (see *Polyzonium*, *Callipus* and *Polydesmus* in text-figs 4*b* and 5*g* and *h*), while a ventral emargination of the distal end of the femur in most groups of Diplopoda and in all Chilopoda facilitates the distal downward bend of the leg. In addition the postfemur may be similarly shaped in fast runners (Nematophora, text-figs 5*g* and 19–21).

In Diplopoda and Chilopoda the prefemur is usually emarginated distally on the

anterior face (text-figs 17*b*, *e*, 21*b* and *Lithobius*, Part 7), while the femur is emarginated distally on the posterior face ; in fast running diplopods the postfemur may be similarly shaped (*Callipus*, text-fig. 21*b*). The anterior prefemoral emargination facilitates a forward flexure of the whole distal part of the leg on the forward stroke ; contraction of the mid-dorsal levator femoris muscle will automatically tend to promote the femur slightly. Similarly the ventral or postero-ventral flexor muscles will tend to flex the leg backwards slightly in the horizontal plane, see flexor postfemoris posterior, flexor tibiae posterior (*fl.po.fe.p.* and *fl.ti.p.* in text-fig. 17*b*) and the corresponding muscles in text-fig. 17*e* and flexor tarsi longus and flexor postfemoris *fl.ta.l.* and (*fl.ta.po.fe.l.*) in text-fig. 21*a* and *b*. These emarginations are most marked in the fastest runners, and it has already been shown (p. 498) how any slight horizontal flexure of the leg both forward and backward will increase the stride and therefore the speed.

An acute flexure at either a hinge or a pivot joint can take place only if the cuticles of the overlapping segments remote from the articulations lie far from one another (p. 516 and text-figs 10*c* and 13). Freely moving pivot joints must be very loose ventrally and dorsally, while hinge joints must be loose ventrally, if they are to allow great mobility ; conversely tighter joints are stronger but less mobile. A loosely articulated leg allows maximum flexures and will suit speedy but not strong movements. It is not surprising therefore to find the legs of strong burrowers to be tightly articulated in the above sense, while those of fast running diplopods and chilopods are loosely articulated, and their segments markedly emarginated in contrast to the burrowers of both groups. The legs of Scolopendromorpha and Lithobiomorpha are flattened antero-posteriorly, a shape giving greatest support to loose joints, a lesser flattening is also seen in many diplopods where it serves the same purpose (text-fig. 17*a* and *b*). A distal widening of segments (*Polymicrodon* femur, text-fig. 20*a*) or a proximal narrowing (*Lithobius* tibia, text-fig. 6*k* and *Polydesmus* prefemur and femur, text-fig. 5*h*) all facilitate mobility at the joints but not strength, and are absent from the Geophilomorpha and most Diplopoda (text-figs 4*a*, *b*, *d* and 6*i*).

In fast runners with longish legs the outstretched position of the leg at the beginning and end of the backstroke is necessarily a weak one since the most rigid parts of the cuticle of the segments scarcely overlap below the hinge joints (see text-fig. 21*a*). This weakness is met in both Diplopoda and Chilopoda by a strengthening of the hinge which becomes elongated transversely across the leg. This can be seen in similar convergent form in the Lysiopetaloidea (text-figs 21*b* and *e*) and in all Chilopoda (Part 7), and contrasts with the small localized hinges of the short segments of the legs of Iuliformia (see text-fig. 17*b*). In the longest legged chilopod, *Scutigera*, the strain on the hinge joints must be greatest, and here an antero-dorsal and postero-dorsal articulation replace the elongated hinge of other chilopods. These double articulations give stability to the hinge joints from prefemur to tibia, and an extra antero-ventral articulation strengthens the still median hinge between tibia and tarsus (see Part 7).

The weakness of the outstretched leg, due to emarginations of the segments, in fast running Chilopoda and Diplopoda is compensated for by the presence of intrinsic protractor and retractor muscles in these groups only, a retractor femoris in *Polydesmus* and *Callipus* (text-figs 5*h* and 21*a*), a protractor postfemoris in *Polymicrodon* and *Callipus* and a protractor tibiae in *Microchordeuma*, *Polymicrodon* and *Callipus* (text-figs 19*a*, *b*, 20*a* and 21). For Chilopoda see Part 7). The photograph of *Polymicrodon*, Pl. 9, fig. 23, does not suggest that these muscles cause a forward and backward bend along the leg in this animal, although the more conspicuous protractors and retractors of the Lysiopetaloidea and fast running Chilopoda may perhaps do so.

The thrust on the ground, leg rotation and pace duration.

A line drawn through the anterior components of the pivot joints and another through the dorsal hinge joints of a diplopod leg indicate the positions of two incom-

pressible axes of the leg. The anterior components of the pivot joints are more robust than are those on the posterior face of the leg (p. 516) and are constructed so as to resist a force tending to telescope the leg segments. As a diplopod leg swings backwards when walking or burrowing, the incompressible axis provided by anterior components of the pivot joints is more or less in line with the thrust exerted against the ground during the middle part of the backstroke. Moreover, the body skeleton is always constructed to transmit such a thrust. The only firm junction between coxa and trunk in the Oniscomorpha is the anterior hinge to the tracheal pouch (Part 4, text-fig. 8f, p. 354) and the procoxa is similarly placed in Chilopoda (text-fig. 6).

Towards the end of the backstroke the dorsal hinge joints in all Diplopoda and Chilopoda become slightly or markedly anterior in position, this firm dorsal axis being brought more into line with the thrust exerted by the extending leg. This change in position of the dorsal hinge line in the Iuliformia is the result of the coxa swinging about an almost horizontal axis; the lower diagrams in text-fig. 3e show the effect of this swing on the positions of the dorsal hinge joints (marked by circles). In the Nematophora the coxa does not swing about an exactly vertical axis as shown in text-fig. 3f, but about an axis passing from below upwards and slightly forwards as indicated in text-fig. 7g, *ax*. This, and possibly small movements of the sternite, result in a slightly forward position of the dorsal hinges during the latter part of the backstroke, in contrast to text-fig. 3f. In the Chilopoda a parasagittal rotation of the coxa about a ventral fulcrum is superimposed upon the locomotory backward and forward swing of the coxa in the horizontal plane (p. 514) and brings the dorsal hinges much further forwards during the backstroke. The ventral edge of the chilopod coxa moves but little, and its dorsal part swings forwards during the backstroke and backwards to a vertical position during the forward stroke, the range of swing increasing with speed; the whole pleural morphology is correlated with this swing (Part 7). By these two coxal movements the Chilopoda combine the effects of the two types of coxal swing found separately in the several orders of Diplopoda; the coxal swing about a vertical axis provides a long stride, as in text-figs 3d and f, while the parasagittal swing of the eucoxa superior adds to the stride by the movement shown in text-figs 3a, b and e. The rotation of the dorsal hinge line forwards during the backstroke strengthens the leg (see below) and a further support is obtained in fast running Scolopendromorpha and Lithobiomorpha by a permanent displacement of the pre-femur-femur hinge to a position just anterior to the mid-dorsal line (text-fig. 6k H.1.).

It is probable that the leg exerts a propulsive force against the ground throughout the backstroke. When running fast the claws of the Scolopendromorpha and Lithobiomorpha, on leaving the ground, swing backwards and towards the middle line before travelling forwards (Part 3, Pls 31–33, figs 13, 18, 30). Such a movement probably would not occur if the latter half of the backstroke was not propulsive. During the first part of the backstroke the leg flexures are increasing, and intrinsic flexors as well as extrinsic retractors provide a motive force, but during the latter part of the backstroke the leg is extending and no distal extensor muscles are present. The distal flexor muscles relax progressively and the thrust on the ground must then be supplied mainly by the extrinsic retractors, but this thrust could scarcely be transmitted effectively unless the dorsal hinge line became slightly anterior in position.

The rotation of the chilopodan coxa in fast running can bring the dorsal hinge line forward during the backstroke to a greater extent than can the fixed axes of coxal swing in diplopods. This may be one of the major factors which has given the Chilopoda their superiority in fleetness over the Lysiopetaloidea which can execute an equally large angle of swing of the leg and as fast a pattern of gait, but use a much slower pace. The latter indicates that either diplopodan muscles are incapable of more speedy movements, or that the extrinsic muscles are too few, or that the skeleto-muscular system will not stand the strain of a more rapid backstroke. The morphology of the slow moving lithobiomorph *Craterostigmus* shows a considerable

but fixed tilted axis of coxal swing which allows hardly any coxal rotation (Part 7), and this aberrant chilopod steps no faster than *Callipus*, thus suggesting that it may be the skeleto-muscular plan and not muscle physiology which determines the speed of stepping in both Diplopoda and Chilopoda.

If pivot joints were situated along the whole length of a leg an increase in skeletal strength would result, but each segment would then need a levator as well as a flexor muscle. If distal levators were present the flexors would have to be smaller and therefore weaker than they are, and such a leg could not exert so strong a pull during the first half of the backstroke. The slightly anterior position of the dorsal hinge line during the latter part of backstroke is therefore of great importance in eliminating a need for distal levator muscles, so enabling the maximum development of flexor muscles in Chilopoda and Diplopoda.

MORPHOLOGY OF LEG SKELETON OF DIPLOPODA AND CHILOPODA SHOWING DETAILED CORRELATIONS OF STRUCTURE WITH FUNCTION.

In both Chilopoda and Diplopoda rigidity of cuticle is required for firm muscle insertions and for directing movement at joints. This is obtained largely by sclerotization in Chilopoda and by more calcification and less sclerotization in Diplopoda (Blower, 1951). Basically slow moving animals, needing external rigidity for pushing, suffer no disadvantage from a heavy skeleton while fast moving chilopods need a light one. Non-elastic unmodified cuticle links the segments, and where this membrane is very short hinges are formed, and adjacent articulating cuticle is strengthened and rendered more elastic by increased thickness and sclerotization.

On basic principles (p. 492) the link between legs and body in Diplopoda might be expected to be mechanically stronger than in Chilopoda, the former serving strong movements and the latter fast ones. This is in fact the case. In diplopods the coxa-sternite articulation is simplest and possibly most primitive in the Colobognatha where the coxal base is wide and not sunk far into the sternite (text-fig. 4*b*). Here and in the Iuliformia and Polydesmoidea the axis of swing of the coxa (*ax.* on text-figs 7*a* and *e*) is fixed by short arthrodial membranes (*v.* in text-fig. 7*e*) on either side of the coxa in the transverse plane. Anteriorly and posteriorly ample arthrodial membrane (*am.* on text-figs 7*d* and *e*) allows the proximal coxal rim to make wide excursions. The body skeleton supports the coxa closely at the axis. In the Colobognatha the lateral union of coxa and sternite is tight, and both are thickened at this point; the mesial union is also tight but less robust. In the Polydesmoidea a sternal boss (*k* on text-fig. 7*e*) and a pleural boss (*t* on text-fig. 13 and Part 4, text-figs 2*e* and 3*f*) of thick cuticle strongly support the mesial and lateral articulations of the coxa, and in the Iuliformia thick sternal and pleural lobes grip the coxal base (white rims of sockets in text-fig. 7*a*).

In the Colobognatha the insertions of the legs on most diplo-segments lie near the hinder margin of the sternite, very little if any rigid cuticle exists behind the legs, the cuticle at this point merging into the intersternite arthrodial membrane. Such a condition could give rise to that of the Oniscomorpha and Nematophora where a tight articulation exists on one side only of the coxal base. An antero-mesial articulation becomes specialized in the Nematophora, and an antero-lateral one in the Oniscomorpha, and in both orders an arthrodial membrane lies behind the coxa. The Chilopoda also have but one link between coxa and body; it is weaker than those of any diplopod but allows great mobility, suitable for the more complex movements of fast runners (p. 509). This freedom needs for its control some 13-33 extrinsic leg muscles (see Part 7). In diplopods there are mechanical difficulties in the accommodation of extrinsic leg muscles (Part 4, p. 328) and a fuller use of skeletal rigidity is necessary both for strength and for control of the joint by a small number of extrinsic muscles. Frequently only two are present, and never more than five.

Diplopod joints between coxa and body with an approximately horizontal axis of articulation.

A simple form of this joint is seen in the Colobognatha (see above). In the Iuliformia a neck near the base of the coxa is gripped in the transverse plane by the rim of the socket, often so tightly that the coxa cannot be removed without breaking the socket, although the latter is widely open posteriorly (text-figs 4a, 7a, *l.p.n.* and 7d posterior leg, where the coxal arthrodial membrane merges into inter-diplo-segmental arthrodial membrane). This brings two advantages over the colobognath condition, a larger angle of swing is possible for the same displacement of arthrodial membrane (see data for Nematophora, p. 514) and the joint is stronger, both suitable provisions for burrowers. Swings of the coxa in the vertical plane of the order of the 60° shown in text-fig. 3e are usual for most Iuliformia, and result in apparent angles of swing of the leg during stepping of $50-65^\circ$, measured in ventral view (see legend to Table I). Such extensive swings would be more difficult mechanically if the coxal base was wider antero-posteriorly than in text-fig. 3e, and the comparable angles of swing during stepping of the Colobognatha *Polyzonium germanicum* and *Dolistenus savi* possessing such a coxa are $45-50^\circ$ and $40-50^\circ$ respectively.

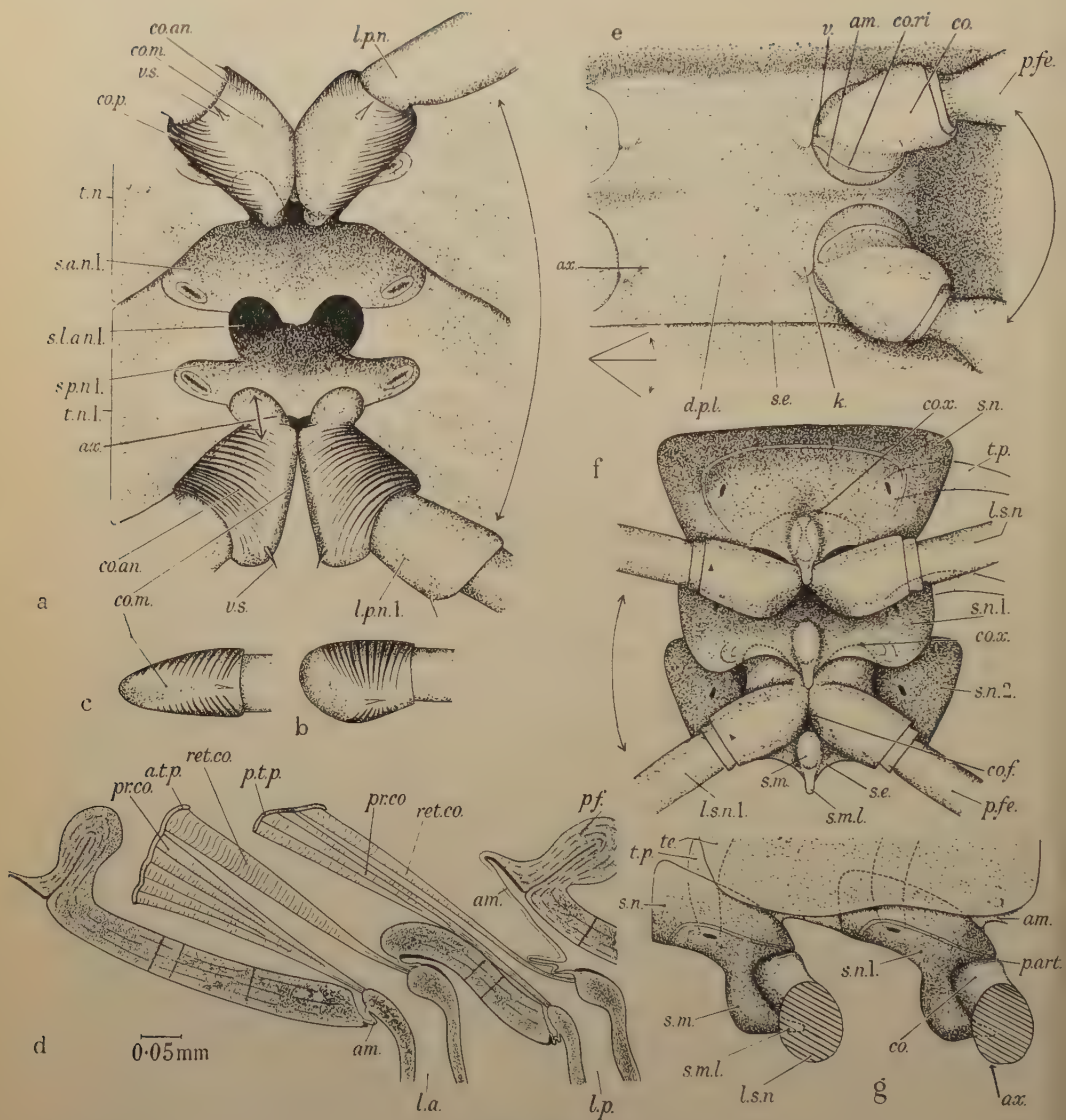
Legs may swing further back than the position terminating the backstroke in running, but not further forward. The most anterior position of the iuliform coxa is shown by the upper leg in text-fig. 7a. The facet *co.m.* is exposed in the forward position. The facet appears as in text-fig. b when halfway through the backstroke and as seen on leg *l.p.n.l.* near the end of it. In the extreme backward position these facets become opposed and invisible, the proximal part of the leg then lying close against the body as in spiralling. The complex shape of the coxa cannot be apprehended clearly in any one aspect. Text-figs 7b and c show the different shapes of the coxa on the anterior and posterior legs of a diplosegment; the coxae neatly fit into the available spaces when spiralling. The axis about which the coxa swings is not exactly horizontal and transverse; from the middle line it tilts slightly upward and backward (*ax.* text-fig. 7a). That this tilt of the axis of coxal swing alone gives rise to the apparently complex movement of the coxa can be ascertained from a working model. The most important result of this tilt is to facilitate an extreme backward swing of the leg so that it lies against the body when the animal spirals.

The coxal articulation with the tracheal pouch in the Oniscomorpha (Part 4, text-fig. 8f) forms a hinge antero-laterally on the coxal rim, the rest of the coxa being surrounded by arthrodial membrane. This very peculiar joint is correlated with the problem of packing the legs into the available space when the animal enrolls (Part 4). The mechanical weakness of such a device is in part compensated for by the broadness of the coxal base allowing a wide spread of the extrinsic muscles (text-fig. 4d), but this solution permits only a small angle of swing of the leg and slow walking.

Diplopod joints between coxa and body with an approximately vertical axis of articulation.

The coxal articulation of the Polydesmoidea is bilateral as in Iuliformia and very strong, see above and text-fig. 7e, and the axis of movement is about 20° short of the vertical, text-fig. 5h.

A tight coxal articulation in Nematophora lies on one side only of the coxal base, but the details are unlike those of the Oniscomorpha. The coxae of *Polymicrodon* in their forward and backward positions are drawn in ventral view in text-fig. 7f, and in lateral view in Fig. 7g. Each sternite, *s.n.* and *s.n.l.* bears a median ventral lobe *s.m.* from which a nose-like projection passes posteriorly to the inner anterior margins of the coxae behind, where it fits into a notch on each (text-fig. 20a, *co.n.*). In *Callipus* oblique flutings on this projection interlock with similar ridges on the edge of the coxa, *co.s.* in text-fig. 21c. In the smaller *Microchordeuma* a single coxal ridge *co.a.* interlocks with the edge of the sternal lobe, text-fig. 19c. Proximally the coxa



TEXT-FIG. 7.

Diagram showing the articulations and the movements between coxa and sternite in Iuliformia, Polydesmoidea and Nematophora.

(a) to (c) A iuliform millipede, *Poratophilus punctatus*, ventral views.

(a) The tergite of ring " $n + 1$ " with its associated sternites is shown with the posterior pair of legs approaching their extreme backward position; the anterior pair of legs is removed to display their sockets, and the tergite and posterior sternite of ring " n " shows the posterior pair of legs in their extreme anterior position. The angular displacement of the legs in the vertical plane is about 50° .

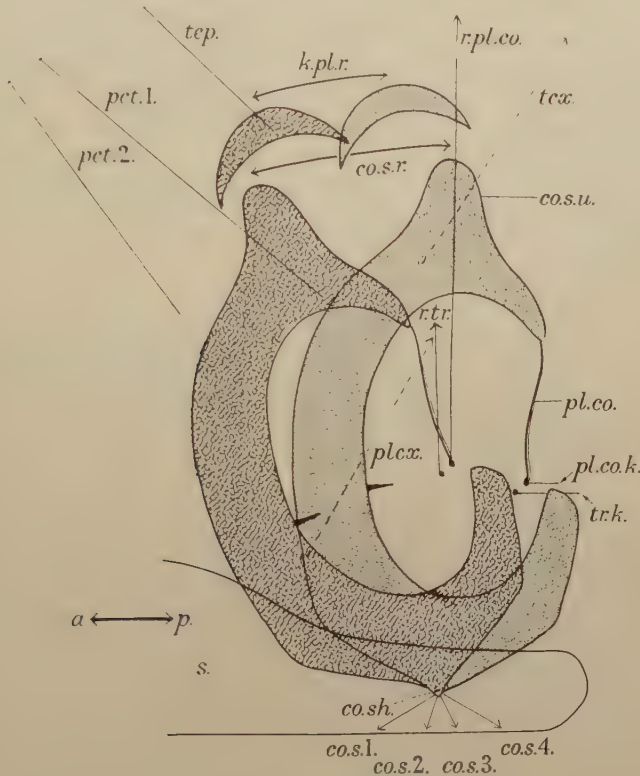
(b) Coxa of posterior leg of ring " $n + 1$ " half-way through a backstroke.

(c) Coxa of anterior leg of ring " $n + 1$ " half-way through a backstroke.

(d) Parasagittal section of *Tachypodoiulus niger* passing through the sternite and the middle of the head of the coxa of the anterior and posterior legs of one ring. Mechanical tint denotes calcified chitin, white surface layer denotes fully sclerotized chitin, black denotes partly sclerotized chitin, arthrodial membranes white.

[Cont. opposite

extends upwards and forwards internal to the main sternal plate (dotted lines on text-fig. 7*f*). The axis of swing of the coxa passes through the interlocking parts of the sternal lobe and antero-median edge of the coxa (*ax* in text-figs 7*g* and 21*d*), the axis sloping upwards and a little forwards. This tilt brings the dorsal hinge line of the leg slightly forwards (see p. 509 for backstroke needs). The most anterior point on the proximal rim of the coxa, (*co.x.*, text-fig. 7*f*), swings outwards and back-



TEXT-FIG. 8.

Diagram, based upon *Lithobius*, to show the parasagittal rotation of the coxa during locomotion which is characteristic of all centipedes. The heavy tint shows the position of the coxa at the end of the backstroke of the leg, and the lighter tint shows the position at the end of the forward stroke. The five muscles which rotate the dorsal end of the coxa forwards during the backstroke of the leg are indicated by straight lines, and the two which rotate it backwards during the forward stroke are indicated by broken lines. The arrows *k.pl.r.* and *co.s.r.* indicate the approximate ranges of movement of the katepipleure and eucoxa superior respectively during fast running.

TEXT-FIG. 7—cont.

- (e) Polydesmoidean millipede *Platyrrhacus* sp. showing the anterior and posterior legs of one side of one diplosegment almost in their extreme anterior and posterior positions respectively, representing an angular displacement of about 60° in the horizontal plane (see side diagram).
 (f) and (g) A nematophoran millipede *Polymicrodon polydesmoides*,
 (f) Ventral view of three sternites, the legs of the anterior two only being drawn, the coxa of leg "*l.s.n.*" is almost at the extreme anterior position, while that of the succeeding leg "*l.s.n.1.*" is at the extreme posterior position. These two positions represent a displacement of 50° in the horizontal plane.
 (g) Lateral view of two sternites drawn from a boiled macerated specimen in which the sternites are pulled apart unnaturally far, the legs are cut off across the coxae.

wards as shown in the diagram, and a wide range of movement occurs laterally between the coxa and sternite where sliding facets ease the rotation, *p.art.* in text-fig. 7g.

The base of the coxa is narrower in *Callipus* than in *Polymicrodon*: the excursion of the lateral rim, corresponding with *p.art.* in text-fig. 7g, will therefore be less for the same angle of swing of the coxa. A narrow coxal base will thus facilitate a wide angle of swing of the leg, but must also make the coxal articulation weaker. If the coxal bases be compared in text-figs 19, 20 and 21, they are seen to become progressively narrower, and the observed angles of swing of the legs recorded from photographs taken in ventral view are 55° , 60° , 65° and 90° respectively for *Microchordeuma scutellare*, *Craspedosoma rawlini*, *Polymicrodon polydesmoidea* and *Callipus longobardius*. The three former animals live in woodland litter and may push with the dorsal surface, although their legs are too long relative to their body width to allow them to burrow in soil (Part 4), but *Callipus* and other Lysiopetaloidea live in rocky places, they are relatively fleetest than any other diplopods and they are the only ones (other than Pselaphognatha), which have not readily pulled a sledge of weights to which they were harnessed and the loads they could be persuaded to shift were less than for *Polymicrodon* (p. 490).

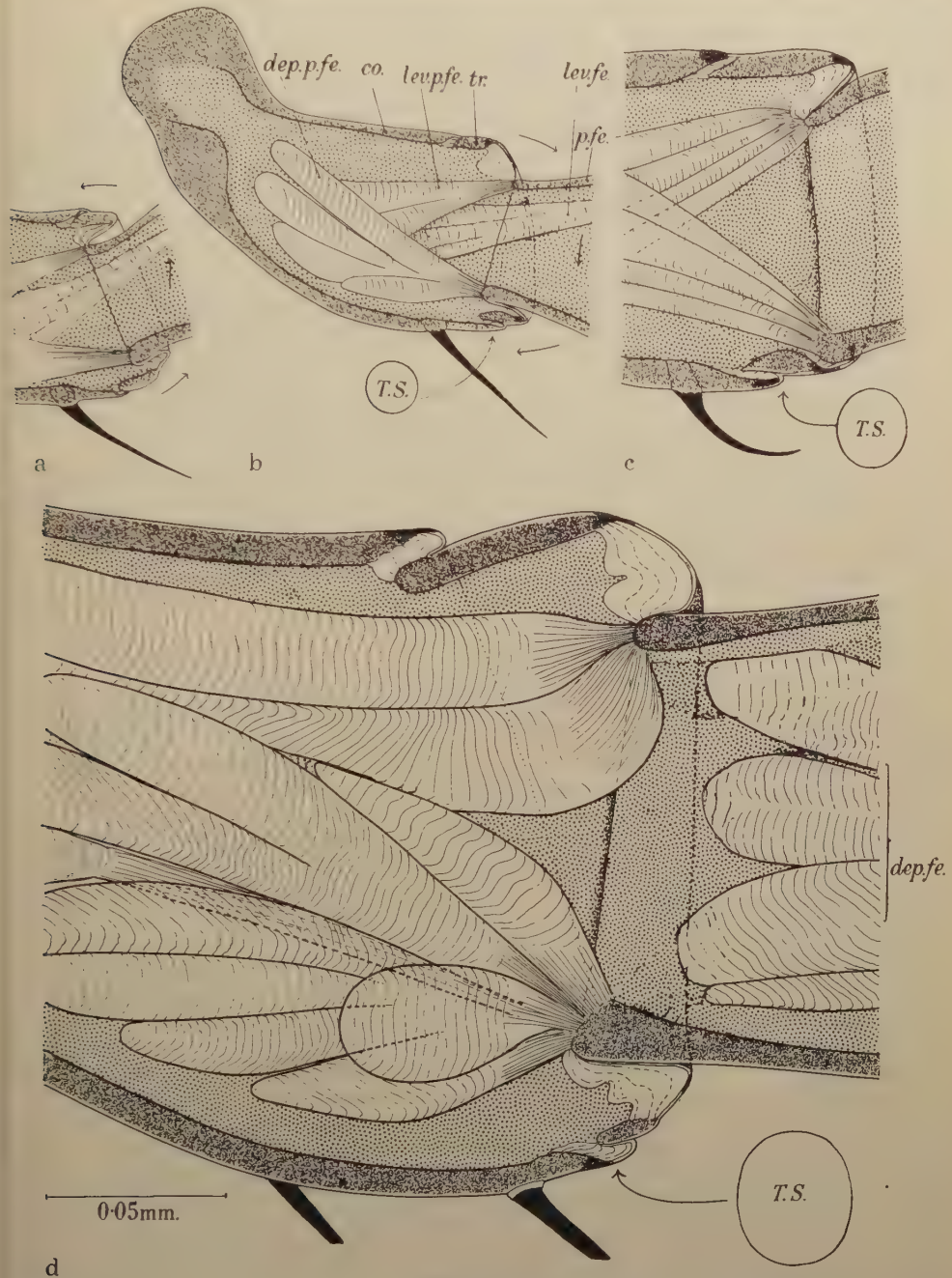
Thus it is probable that the narrow coxal base in the Lysiopetaloidea is correlated with an ability to move the legs through a larger angle of swing and to achieve greater fleetness than in other diplopods, and the reluctance of Lysiopetaloidea to pull a sledge probably indicates a degree of leg weakness not shared by *Polymicrodon* and other Nematophora. The contrast between the coxal joints of *Polymicrodon* and *Polydesmus* suggests that the latter is much the stronger and the force put out by the leg of *Polydesmus* is much greater than that of *Polymicrodon* (Part 4, Table I).

Chilopod joints between coxa and body.

All four groups of Chilopoda show a basic similarity in the union between coxa and body. Figures of the pleural regions will be found in Part 7, only the general features being given here. Descriptions of the coxa are to be found in all monographs on Chilopoda (Attems, 1926 etc.), but although these are correct as far as they go, they do not serve as a basis for functional considerations.

The coxa is very short in all orders (see p. 506). Ventrally it articulates with the sternite (*co.sh.*, text-fig. 8, with the pro- and metacoxa in Geophilomorpha), and muscles *co.s.1.-co.s.4.*, fanning out on to the sternite anteriorly, posteriorly and mesially, hold the coxa in place. Dorsally a lobe from the coxa, the eucoxa superior, *co.s.* projects far above the leg as a flat plate, extending more than half-way up the pleuron in *Lithobius*. The coxa forms an incomplete cylinder in all orders, being open on the postero-dorsal sector. This is more or less closed by the pleurocoxa, which forms a triangular sclerotized zone in the Geophilomorpha, a narrow bar extending downwards and backwards from the postero-dorsal corner of the eucoxa superior in Scolopendromorpha and Lithobiomorpha (text-fig. 8) and a more solid scute articulated at both ends to close the coxal ring in the Scutigermorpha.

The only localized articulation between coxa and body in *Lithobius*, for example, lies at the fulcrum of movement where a short arthrodial membrane links a mid-ventral coxal thickening with a robust sternal concavity, *co.h.* and *s.h.* on text-fig. 11a. Elsewhere the coxal cuticle merges into either the flexible pleural cuticle or the deep folds of arthrodial membrane joining the coxa loosely with the pro-, meta- or pleurocoxa. This looseness of attachment permits the two movements of the coxa which are executed together, an antero-posterior swing causing the main stepping of the leg, and the rotation in the parasagittal plane (p. 509) which brings the dorsal hinge line of the leg forwards. This rotation is shown diagrammatically on text-fig. 8. The pleurocoxa of *Lithobius* ends in a small sclerotization *pl.co.k.* closely associated with another on the proximal rim of the trochanter *tr.k.* text-figs. 8 and 11a. Both serve for muscle attachments, and both lie more dorsally



TEXT-FIG. 9.

Posterior views of the proximal part of the legs, the cuticle being drawn in sagittal section, to show the trochanter and its joint with the coxa and prefemur in Iuliformia of different sizes. Muscles with insertions within the field are drawn. The rings "T.S." show the shape of the trochanter in transverse section. Mechanical tint represents calcified cuticle, the white superficial layer denotes fully sclerotized cuticle, black indicates partly sclerotized cuticle and the interrupted lines show unmodified cuticle of arthrodial membranes.

- (a) and (b) *Blaniulus guttulatus* with prefemur elevated in (a) and depressed in (b).
 (c) *Cylindroiulus londinensis*.
 (d) *Schizophyllum sabulosum*.

when the coxa swings forwards during the backstroke of the leg than they do in the opposite position. Muscles pulling vertically upward on these two points *r.t.r.* and *r.pl.co.* will assist in the forward swing of the eucoxa superior just as much as muscles *pct.1.* and *pct.2.* sloping antero-dorsally (see p. 543).

Pleural scutes are also involved in the rotation of the coxa. A forward and backward movement of the katopleure, pulled forward by muscle *tep.*, will crumple the soft pleuron in a manner helpful to the coxal swing (text-fig. 8). The movement is damped out dorsally by the anopleure and tergite, and by corresponding scutes in other orders.

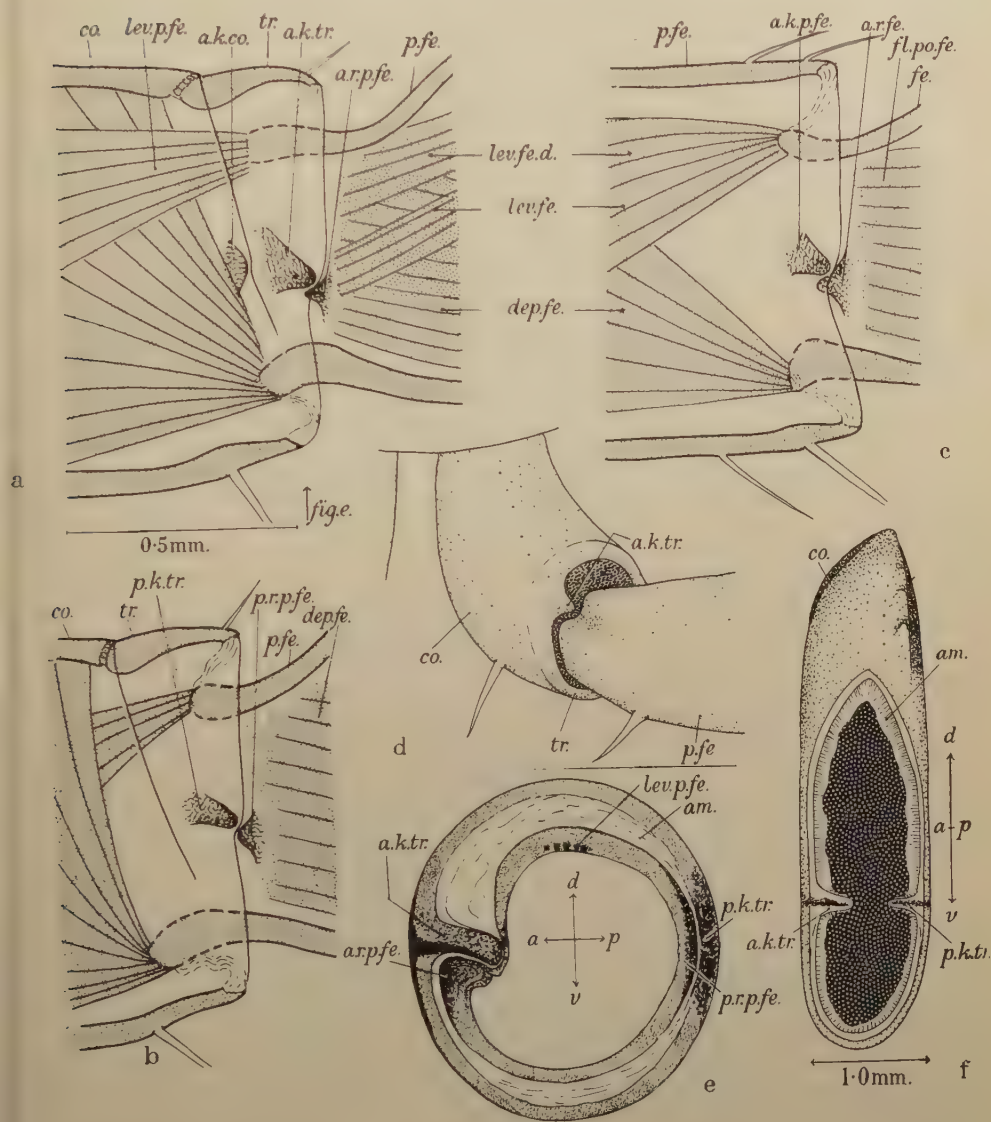
The narrow form of the pleurocoxa in Scolopendromorpha and Lithobiomorpha serves a special need. The survey of diplopodan legs and joints has shown the existence of a difficulty of leg design allowing a wide angle of swing of the leg. The chilopodan solution of this problem is quite different from that found in the Lysioptaloidea. The incompleteness of the coxal cylinder and the narrowness of the pleurocoxa brings the proximal posterior rim of the trochanter close to the flexible pleuron. Retractor and rotator muscles pull on this rim. A large angle of swing of the leg is obtained partly by the protractor-retractor coxal swing, and partly by an added backward movement of the trochanter which deforms the flexible pleuron behind the leg. The coxa-trochanter joint (see below) which allows this movement is very mobile but weak. The long legs of *Scutigera* have necessitated a strengthening of this joint and an increased rigidity of the pleurocoxa, but these things have limited the angle of swing of the leg which is less than in any other chilopod.

Pivot joints and trochanter of chilognath Diplopoda.

Freedom of movement (see p. 508) at a pivot joint results from long dorsal and ventral arthrodial membranes between well separated rigid parts of trochanter and prefemur cuticles (text-fig. 9d), while the tighter joint between coxa and trochanter (text-fig. 9a-d) allows less movement. The chilopod coxa-trochanter joint is looser still, and permits greater flexure than does any diplopod pivot joint; note the great expanse of arthrodial membrane *am.* in text-fig. 11a, compared with 10e.

A simple form of pivot joint is seen in *Blaniulus* between trochanter and prefemur, text-fig. 10d. A knob-like inner projection from the anterior side of the trochanter in the middle of the distal end fits into a corresponding depression on the proximal anterior end of the prefemur. With increase in size the pivoting articulations become relatively larger and stronger. Text-fig. 10a and b shows the articular components of a spirobolid on the anterior, *a.k.tr.*, *a.r.p.fe.*, and posterior, *p.k.tr.* and *p.r.p.fe.*, faces of the leg between trochanter and prefemur. The knob-like proximal components of the pivot are larger and browner than in *Blaniulus*, and they fit above and against an articulating depression and ridge on the prefemur. The prefemur-femur pivot is similar. A transverse section across the trochanter-prefemur joint of *Tachypodoiulus niger*, text-fig. 10e, shows the anterior pivot *a.k.tr.* and *a.r.p.fe.*

The anterior components of pivot joints are always more robust than are those on the posterior face of the leg, compare the anterior and posterior trochanter-prefemur pivots in text-fig. 10a and b. In *Tachypodoiulus* the posterior component is feebly developed and is represented by closely associated highly sclerotised areas, text-fig. 10e *p.k.tr.* In all orders except the Oniscomorpha the anterior components of pivot joints *P.1.-P.3.* are present from the coxa to the femur (text-figs 4 and 5). Even if the coxa-trochanter joint is immobile, because these two segments are partly fused, the remains of a non-functional pivot articulation is represented by a small knob (*a.k.co.* in text-fig. 10a) with nothing to work against. This surely is clear evidence of a secondary elimination of the coxa-trochanter mobility. In the Oniscomorpha the coxa and trochanter are more completely fused than in the larger Iuliformia and the very short arthrodial membrane seen dorsally and laterally but not ventrally between these segments in text-fig. 10a has vanished. No trace of pivot 1 remains



TEXT-FIG. 10.

Diagrams showing the trochanter in large iuliform millipedes and the pivot joints of diplopodan legs. Conventions as in text-fig. 9.

(a) to (c).—A large spirobolid sp. (large Spirostreptomorpha are similar).

(a) Anterior face of the leg showing anterior components of pivot joints P.1. and P.2. (see text-fig. 4a).

(b) Posterior face of the same showing posterior components of pivot joints,

(c) Anterior face of the leg showing anterior components of pivot joint P.3. (text-fig. 4a).

(d) Oblique view of anterior pivot joint P.2. of *Blaniulus guttulatus*.

(e) Transverse section of leg of *Tachypodoiulus niger* at the level shown by the arrow "fig. e" in fig. a to show pivot joint P.2.

(f) Distal end of a disarticulated coxa of the oniscomorph *Sphaerotherium giganteum* showing proximal components of pivot joint P.2.

and the apparent coxa-prefemur pivot represents the pivot between trochanter and prefemur of other diplopods. It is very strongly constructed, as shown by the end on view of the distal part of the fused coxa and trochanter of *Sphaerotherium* in text-fig. 10*f*, *a.k.tr.* and *p.k.tr.*

A posterior component to the pivot joint between coxa and trochanter is absent from all orders except the Polydesmoidea and Lysioptaloidea where its presence must confer added strength to the respectively stout and mobile leg (text-figs 5*g*, *h* and 19*d*). The posterior component of the trochanter-prefemur pivot is always present, while that of the prefemur-femur pivot occurs only in the Nematophora and must be concerned with the conspicuous mobility, often combined with a litter-living pushing habit. This distribution of pivot components suggests that greatest strain and mobility lies at the trochanter-prefemur joint where the major lift of the leg takes place (text-figs 4-5).

The evolution of the trochanter has been outlined in general terms (p. 506) and details concerning its specializations in diplopodan orders may now be considered. The Colobognatha and small Iuliformia such as *Blaniulus* (text-figs 4*b*, 9*a* and *b*) show limited movement between coxa and trochanter when the distal part of the leg is raised and depressed. In larger Iuliformia, coxa-trochanter mobility decreases as does the length of the ventral face of the trochanter (compare text-fig. 9*a*, *b*, *c* and *d* drawn to the same scale); and in Spirostreptomorpha and Spiroboloidea the ventral parts of the trochanter become fused with the coxa (text-figs 10*a* and *b*). Fusion is complete in the Oniscomorpha. Strong slow movements, or almost permanent flexures (text-fig. 4*d*) appear to have led to a merging of the coxa and trochanter.

The greater mobility of the trochanter in the fleetier Polydesmoidea and Nematophora gives very free levator and depressor movements (compare text-figs 9*a* and *b* with 12, and see 19*d* and 20*c* and *d*). Greatest strides from long legs require a large range of flexures at the joints (p. 503) and in both groups there is plenty of room for movement of the proximal rim of the trochanter within the distal part of the coxa dorsally and ventrally. In *Polymicrodon*, text-fig. 20*c*, the coxa can slide dorsally over almost the whole trochanter when the leg is raised, but not more than a third can be covered by the coxa in *Blaniulus*. In *Polydesmus* the distal edge of the rigid coxal cuticle is marked by one black dot and the middle of the trochanter by two dots on text-fig. 12. When the leg is raised the whole trochanter is covered by the coxa dorsally, and when it is depressed the trochanter is similarly invisible ventrally. The narrowness of the proximal part of the prefemur relative to the diameters of the trochanter and coxa make possible the wide range of trochanter-prefemur flexures.

The flexures at either end of the trochanter in the Polydesmoidea exceed those of any other diplopod, and they are achieved without loss of strength. Text-fig. 13 shows a vertical section of the leg base, levator prefemoris being drawn above and depressor prefemoris below (see text-fig. 5*h*), and single and double black dots are placed as on text-fig. 12. The rigid trochanter cuticle is morphologically much shorter than in any other diplopod, so short in fact that its thickness greatly exceeds its length. The ducts of the epidermal glands which traverse the cuticle are black in the figure, conspicuous ducts lie dorsally between the ectodermal epithelium and cuticle surface opposite the double dots, and exactly resemble the typical ducts shown in the ventral coxal cuticle. The conically shaped trochanter must be more rigid than a cylindrical short segment would be, and the pivot articulations, morphologically at either end of the trochanter, are now almost one over the other.

Arthrodival membranes between segments are often thicker than the sclerotized cuticle to which they are attached (text-figs 9*d* and 14). In the Polydesmoidea the arthrodival membranes at either end of the trochanter are divided into surface, *o.a.m.*, and deep, *i.a.m.*, layers separated by a fluid filled space, *s.co.tr.* and *s.tr.p.fe.* These spaces, like the synovial cavities of mammalian joints, both ease the movements and strengthen the joint. Synovial cavities are present at all leg joints of Polydesmoidea and have not been found in any other myriapods. A similar space *s.r.co.*, bounded

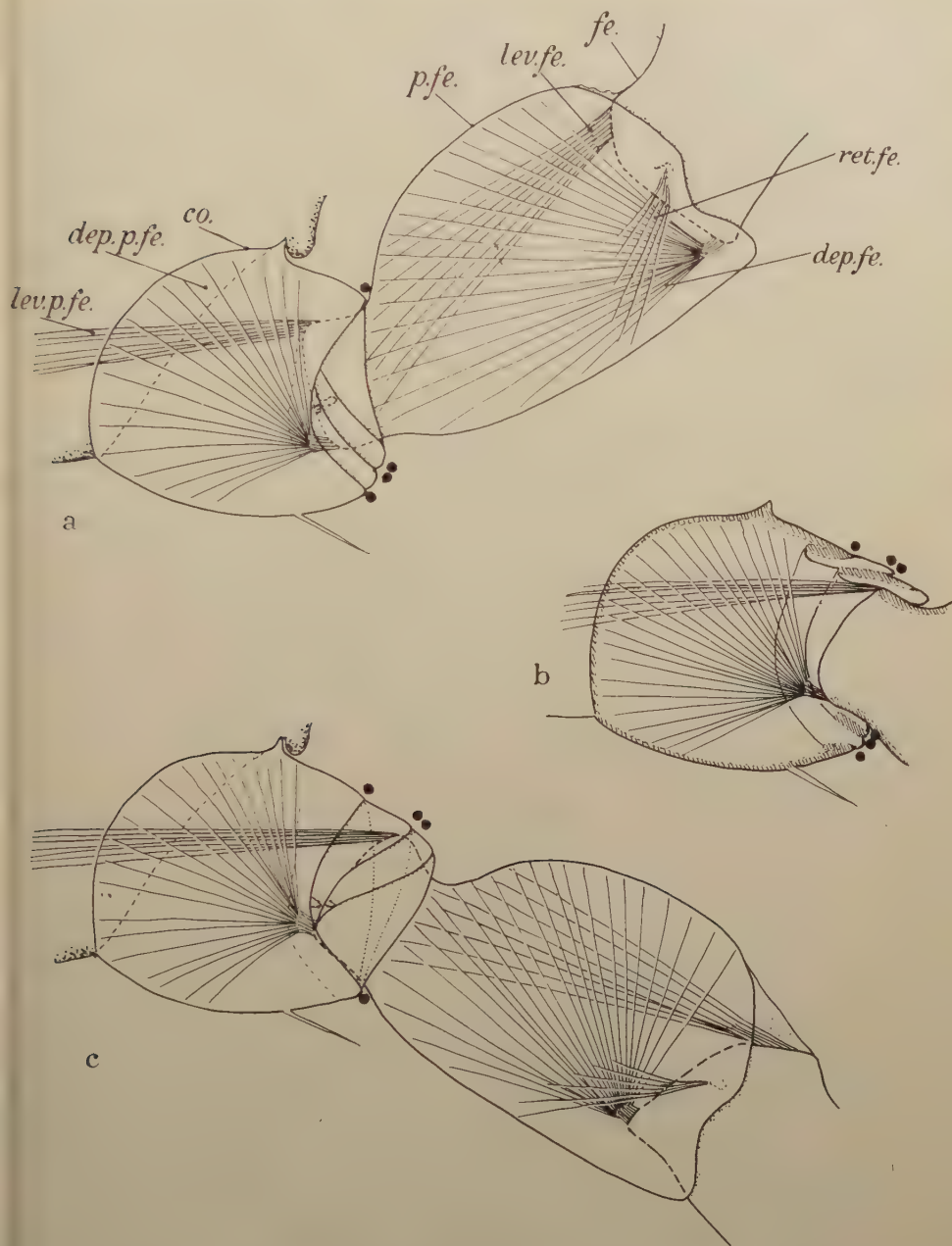
by inner and outer lamellae of arthrodial cuticle, is seen at the joint between coxa and ring, text-fig. 13. The occurrence of these synovial cavities in the order of diplopods which exerts the strongest leg movements is significant.

There are many diagrams of the coxa-trochanter region of Polydesmoidea in the systematic literature which bear inconsistent numbers of transverse lines. The rigid cuticles of the coxa and trochanter merge distally into arthrodial membranes and the coxal cuticle thickens greatly proximal to these points (text-fig. 13). A cleared whole mount of a leg may show a number of lines corresponding with the levels 1-6; not all will catch the eye in one preparation, a line at level 3 for example will become apparent only when the telopodite is elevated, and this section of arthrodial membrane becomes more bent. Most of these lines are difficult to follow because of the alterations in the already complex trochanter on the anterior and posterior faces where the pivoting articulations lie. The morphology of these joints cannot be apprehended without microtome sections.

The pivot joint and trochanter of Chilopoda and the evolution of the chilopodan coxa and pleurocoxa.

The superficial differences between the coxa-trochanter union in the Chilopoda and a diplopod pivot joint are so striking as to mask their fundamental similarity. The basic form of the chilopod pivot is shown in text-fig. 11a where the trochanter is cut off near its base and the ventral projecting part of the coxa is foreshortened. The anterior component of the chilopod pivot is greatly elaborated, its principal parts being shown in black in the figure. A Y-shaped brown sclerotized rib, lying in the cuticle of the coxa, is hinged to a sclerotized bar in the trochanter (*y* and *tr.b.*). The stem of the Y is more or less at right angles to the rest, and lies in the parasagittal plane across the wide arthrodial membrane separating the two leg segments; here the arms of the Y originate. One passes forwards and upwards near the morphologically distal edge of the eucoxa superior where it fades out. The other arm is the larger, it sweeps forwards and downwards, crossing the coxa as the well known costa coxalis *c.c.*, and passing close to the proximal coxal margin, fades out near the fulcrum between coxa and sternite. The costa-coxalis is often shielded externally by a flange of coxal cuticle which appears to protect this vital structure. The trochanter bar *tr.b.* is essentially radial to the trochanter and articulates closely with the stem of the Y, sometimes lying in a groove of the latter and sometimes situated less closely, but the articulation is always a horizontal hinge allowing very free levator and depressor movements of the distal part of the leg. The articulation is complex and strong for its size, although narrow and flexible, and it is the only firm union between the coxa and the distal part of the leg.

The proximal end of the trochanter of chilopods differs from that of other leg segments in that the rigid cuticle does not form a firm rim but gradually merges into the arthrodial membrane (text-fig. 11b). No such condition occurs in Diplopoda. This feature probably eases the very wide excursions made by this margin (see below). Near the proximal limit of the trochanter lies an annular cuticular thickening which serves two functions. Strong intrinsic and extrinsic muscles are attached to it, and in the Scolopendromorpha and Lithobiomorpha a transverse breaking plane lies across it. An injured leg, which might interfere with the gait, can be detached from the body by separation of the annulus into proximal and distal parts. A small strongly sclerotized rib in the trochanter cuticle extends approximately at right angles from the bar *tr.b.*, passing across the trochanter to merge with the proximal annulus, so linking a major skeletal unit of the trochanter with the anterior pivot, now a hinge joint, and the costa coxalis. The annulus thus makes it possible for a long limb to be supported by only a narrow hinge set at right angles to a point on the proximal rim of the trochanter. Such a coxa-trochanter articulation is clearly suitable for rapid weak movements and not for strong ones.



TEXT-FIG. 12.

Posterior views of the proximal leg segments of *Polydesmus angustus* showing the intersegmental movements.

The single black spots mark the distal dorsal and ventral limits of the rigid parts of the coxa, and the double black spots mark the middle of the furrow on the trochanter (see also text-fig. 13).

(a) The prefemur elevated to a maximum.

(b) Optical section of skeleton of proximal part of limb, prefemur horizontal.

(c) The prefemur depressed to a maximum.

Both parts of the anterior hinge could have evolved from some simple pivot. The anterior pivot of *Tachypodoiulus* in text-fig. 10e shows a Y-shaped highly sclerotized zone staining red with Azan (black in the figure), with the stem of the Y set at right angles to the coxal face and the arms spreading a little way up and down the latter. The posterior components of the pivot in text-fig. 10e, *p.k.tr.* and *p.r.p.fe.*, are less elaborate and appear as two closely associated zones of brown sclerotized chitin, although a better formed component is seen in larger species (text-fig. 10b). In *Lithobius*, text-fig. 11a, a thickening, *tr.k.*, on the posterior side of the proximal annulus of the trochanter lies opposite the knob on the end of the pleurocoxa, *pl.co.k.*, the two being separated by arthrodial membrane. Comparison with text-fig. 10e indicates that these two knobs represent the posterior components of a pivot joint, its articulation being now extremely loose. It may be suggested that the pleurocoxa is in reality a modified part of the true coxal cylinder, and is not comparable with pleural scutes such as the pro- and metacoxa, katopleure and anopleure (see Part 7).

The narrow mobile pleurocoxa of Scolopendromorpha and Lithobiomorpha and the very loose remains of the posterior component of the coxa-trochanter pivot joint both contribute to the very large angle of swing of the leg (p. 516). It is probable that the "incomplete coxal ring" and the narrow pleurocoxa are not primitive features, but are specializations correlated with fleetness. A secondary union of pleurocoxa and coxa has become necessary in *Scutigera* because of leg length and the need for increased stability at its base, and a tighter, stronger posterior component of the coxa-trochanter pivot has been necessary for the same reason (Part 7). Both these changes have reduced the angle of swing of the leg (Table I), a loss compensated for by great length of leg. The large pleurocoxal sclerotization of the Geophilomorpha is clearly associated with secondary specialization for a burrowing habit (Part 7).

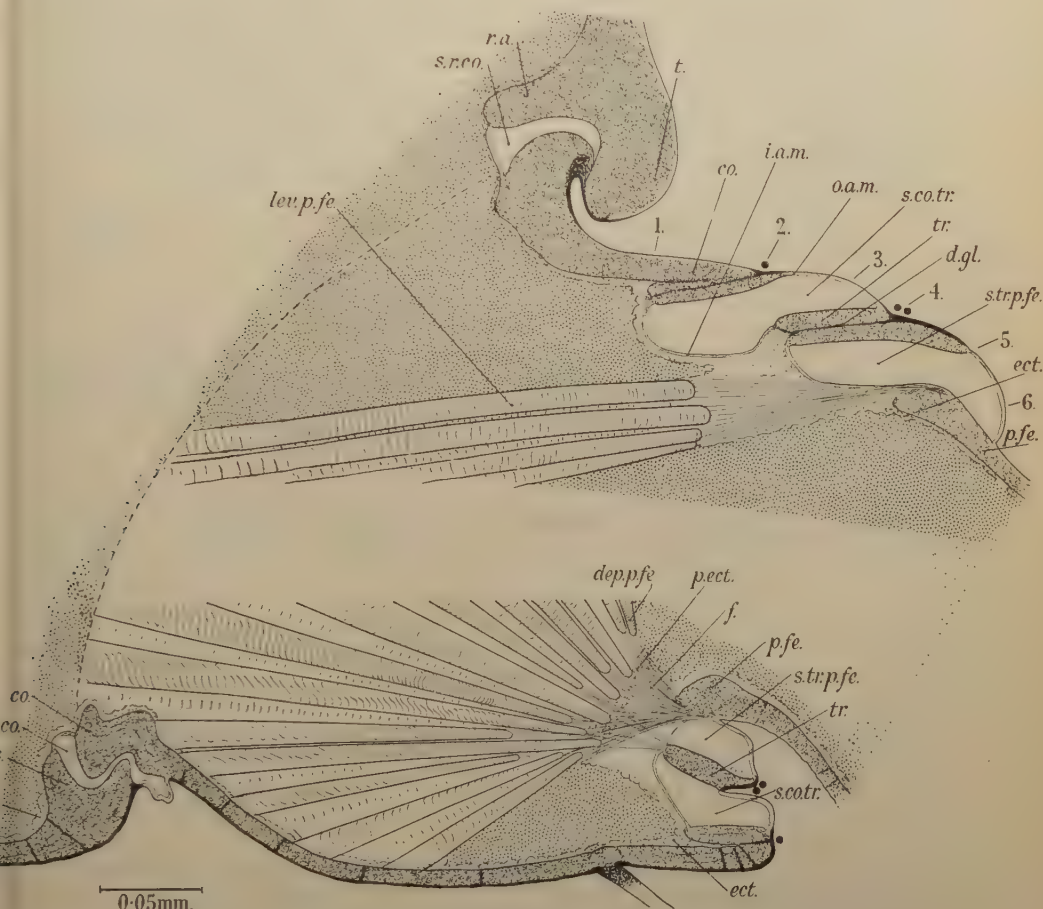
Leg specialization in diplopods has led either to great mobility of the trochanter or to its fusion with the coxa in correlation with locomotory needs. The fusion of the chilopod trochanter with the prefemur in the three fleeter orders facilitates the raising of a longer leg than is possessed by Geophilomorpha (p. 507), but the nature of the junction between these segments suggests that another need is also served. Text-fig. 11b shows a vertical section of the trochanter of *Lithobius*. Distally the trochanter is strongly curved, and near the junction *j.tr.p.fe.* the trochanter cuticle is composed of a surface and a deep layer of sclerotized cuticle staining red with Azan separated by a middle layer of unsclerotized cuticle, staining blue, which passes into the narrow remnant of an arthrodial membrane between the two segments. The latter is too short to allow much play between the segments. Sclerotized thin cuticles staining red with Azan are conspicuously elastic in the galea of butterflies (Eastham, 1955) and the adhesive lappets on the claws of *Polyxenus* (Part 5). The distal dorsal part of the trochanter is probably more elastic than other parts of the leg, allowing a slight telescopic distortion in this region. Legs as small as those of chilopods probably do not need the bulk of elastic tissue corresponding to those of the fleeter mammals, but the occurrence of a region such as just described in fleet centipedes only, while the trochanter-prefemur joint of the Geophilomorpha resembles any normal hinge joint of a diplopod or chilopod, suggests that an elastic function may be present. Marey (1895, p. 162) referred to the importance of elastic tissue for conserving energy in vertebrates which can be used to give the highest jumps and fastest speeds (see also Maynard Smith & Savage, 1956 and others), and it seems likely that the trochanter may serve a comparable function in fast running centipedes.

The pivot joints and trochanter of Pselaphognatha.

The evolution of an anterior hinge between coxa and trochanter in the Chilopoda with a conspicuous Y-shaped coxal component results in a larger angle of swing of the leg than is possible to most Diplopoda. The Pselaphognatha have evolved a

comparable hinge and can swing their legs through approximately 90° (Part 5, text-fig. 5a). Since they do not push, their legs no longer need the strong construction necessary to their diplopodan ancestors.

The anterior components of the three pivot joints of diplopods are united to form the Y-shaped skeleton on the anterior face of the leg in *Polyxenus* (text-fig. 4c and Part 5). The arms of the Y extend morphologically upwards and downwards on the anterior face of the coxa, as in Chilopoda, and in a similar manner serve for muscle attachments and for support of the hinge between coxa and trochanter. The only difference lies in the fact that there are three hinges across the stem of the Y at the coxa-trochanter, trochanter-prefemur and prefemur-femur junctions instead of one.



TEXT-FIG. 13.

Diagrammatic vertical section of the coxa and trochanter of *Polydesmus angustus* to show the nature of the trochanter and its articulations. Part of the levator prefemoris is shown above and part of the depressor prefemoris below (see text-fig. 5h for the full extent of these muscles). The prefemur is depressed, much as in text-fig. 12c so that the trochanter is covered ventrally by the coxa. Conventions of the cuticle as in text-fig. 9, and the black spots as on text-fig. 12.

Thickened ectodermal epithelium contains the tendinous fibrils attaching muscle fibres to the cuticle, and a line of ectodermal pigment, *p.ect.* lies deep in the limb close to the muscle fibres.

The trochanter and prefemur are short, cylindrical and of different diameters, and ample arthrodial membrane lies between them and between the coxa and trochanter (text-fig. 4e and Reinecke, 1910). This means that great flexibility exists at these joints, which can tip into one another on all sides except where the Y-skeleton lies,* a remarkable parallel evolution to the Chilopoda.

Hinge joints between leg segments of Diplopoda and Chilopoda.

Hinge joints are constructed basically in a similar manner in chilopods and diplopods, but show variations suiting the functional needs of the legs. Successive leg segments are united by the thin superficial fully sclerotized cuticle (white in text-fig. 14a and b). The thick, partly sclerotized or calcified cuticles of each segment are discontinuous (mechanical tint in text-fig. 14) ; dorsally a small amount of unmodified cuticle (white with interrupted lines in the figures) lies between, and expands into the ample arthrodial membrane situated laterally and ventrally. This membrane is very flexible and non-elastic, although it may be thick. The rigid cuticle of each segment becomes gradually thinner distally. The apparent distal edge of a segment depends on how far the arthrodial membrane is infolded, and on the point at which the attenuated, partly sclerotized cuticle is bent. The range of movement of a hinge joint is indicated on text-fig. 14b.

In the vicinity of the dorsal hinge, and often all round the distal extremity of the partly sclerotized cuticle, increased sclerotization is apparent both by the amber colour of the cuticle and by the greater affinity for red colouring after Azan staining. A diplopod in which the thick limb cuticle stains dark blue, as opposed to the light blue of arthrodial membranes, may show the red colour in the zones indicated by black in text-fig. 14a and b. It is probable that this extra sclerotization provides elasticity which will avoid permanent deformation at the tight hinge, and may assist slightly in the unbending of the distal edge of the segment when the leg stretches out. These red staining zones are not continuous from one segment to the next and do not provide an elastic force capable of unflexing the leg, as can be ascertained by manipulation of the skeleton.

At the incomplete joint across the tarsus in the Lysiopetaloidea the arthrodial membrane is absent dorsally where the sclerotized cuticle is undivided. At the hinge region lies a slightly thickened patch of extra sclerotization (text-fig. 14E) which is probably elastic, so forming an incipient hinge, H.4. The amplitude of movement must be small because the arthrodial membrane is short ventrally. This joint is clearly at an early developmental stage of joint formation compared with the other hinge joints, in contrast to the disappearing joint between coxa and trochanter in large Luliformia.

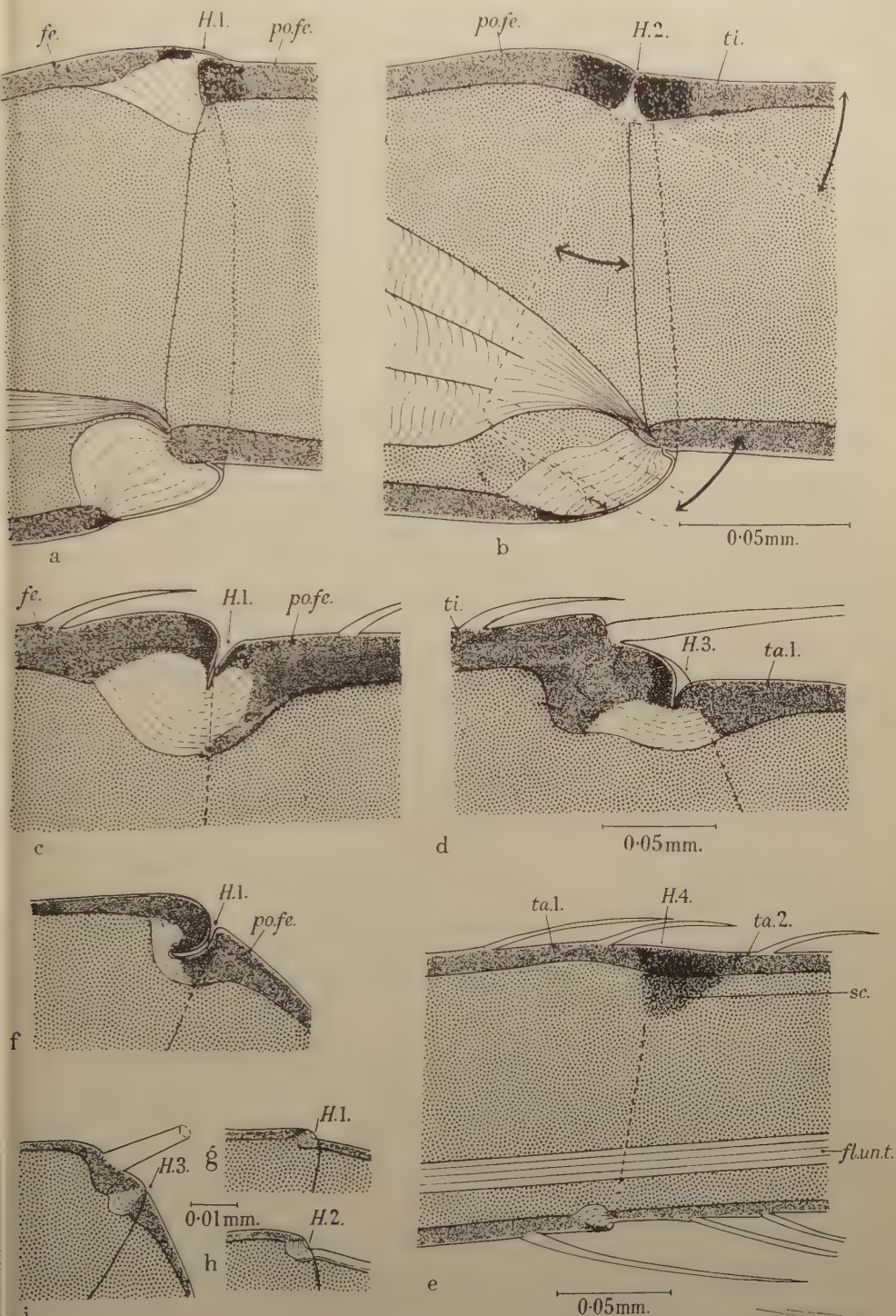
* In Part 5, p. 167, the mobile trochanter was erroneously likened to a "universal joint".

TEXT-FIG. 14.

Text-figs 14 and 15 show the hinge joints between the segments of the legs of Diplopoda.

The positions of H.1.-H.3. are indicated by rings on text-fig. 4a, and H.4. is the incomplete joint across the tarsus of the Lysiopetaloidea. Conventions as in text-fig. 9.

- (a) *Schizophyllum sabulosum*, joint between femur and postfemur.
- (b) *S. sabulosum*, joint between postfemur and tibia, the arrows and dotted lines indicate the flexed position of the tibia, but the infolded intersegmental cuticle is omitted in this position.
- (c) to (e) *Callipus longobardius* : (c) joint between femur and postfemur, (d) joint between tibia and tarsus 1, (e) joint between tarsus 1 and tarsus 2. The extent of the sclerotized cuticle spreading on to the anterior and posterior face of the leg is shown by "sc."
- (f) *Polymicrodon polydesmoides*, joint between femur and postfemur.
- (g) to (i) *Microchordeuma scutellare* : (g) joint between femur and postfemur, (h) joint between postfemur and tibia, (i) joint between tibia and tarsus.



TEXT-FIG. 14.

The mid-dorsal tightness of the joint varies, compare the femur-postfemur joint with that of the postfemur-tibia of an iuliform millipede in text-fig. 14a and b, but in most diplopods the tightest part of the joint is a mid-dorsal point as shown in text-fig. 17b. Where either greater force or greater speed is exercised by the leg the joint becomes modified. In both Chilopoda and Nematophora a larger angular displacement occurs at the hinge joints (p. 508) and in both groups the fully sclerotized surface layer of cuticle is tucked in at a transversely elongated dorsal hinge (text-figs 14c, d and f and 21b and e); the partly sclerotized cuticle on either side of the infolding stains red with Azan. In Chilopoda and in the fleet *Callipus*, a fair amount of dorsal arthrodial membrane supplies the deformable part of the hinge, which may receive some support also from inwardly directed thickenings of the partly sclerotized layer (text-fig. 14c and d). In diplopods which push as well as employing wide angular displacements at the hinge joints, extra strength is obtained by the intucked surface layer curving inwards and forwards, and a lesser amount of arthrodial membrane lies at the hinge. This is seen in *Polymicrodon* (text-fig. 14f) and more markedly in the larger leg of *Polydesmus* (text-fig. 15k) where the infolding is so great that the distal segment curls upwards to grip the edge of the proximal segment, and the opposing sides of the intucking show extensive regions staining red to purple with Azan. *Microchordeuma* probably pushes but little if at all (Part 4) and its hinge joints lack the intuckings seen in *Polymicrodon*, compare text-fig. 14g-i with f.

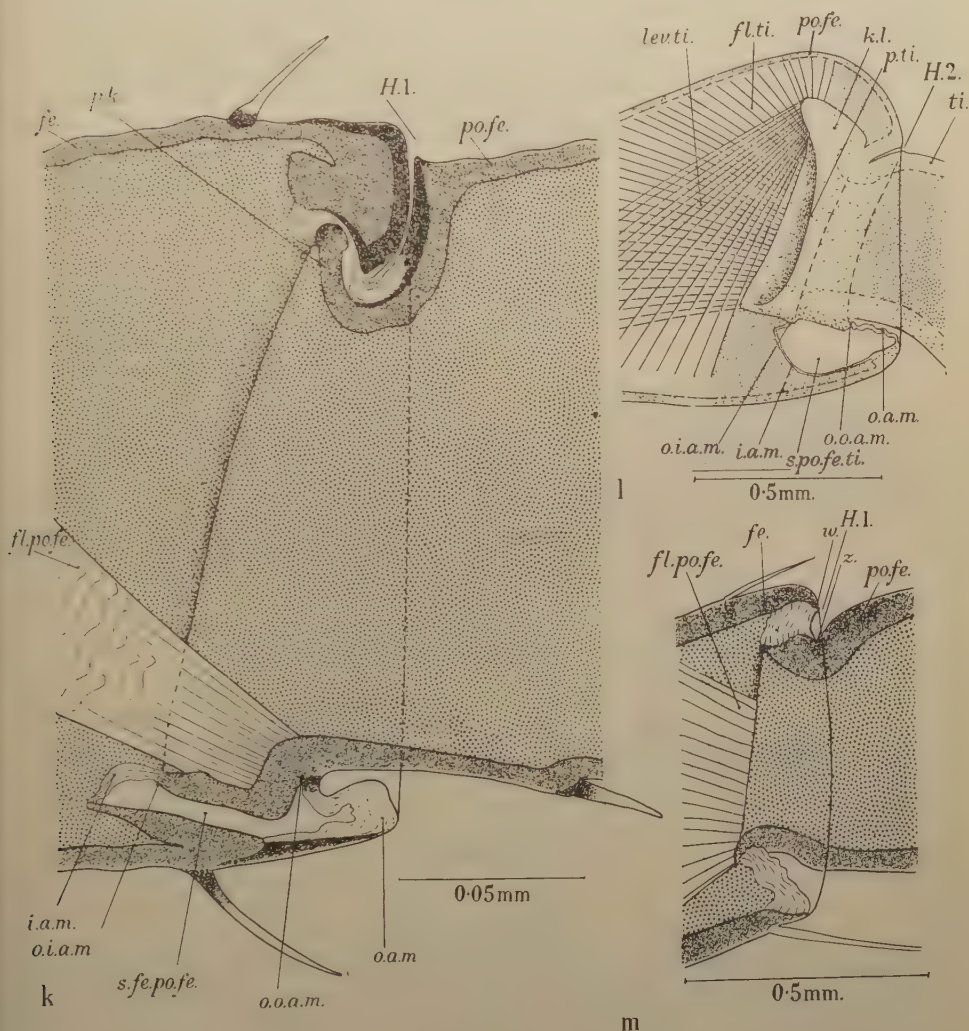
The greater elaboration at the dorsal hinge of the leg of *Polydesmus* extends all round the joint. Ventrally and laterally, the partly sclerotized cuticles of the two segments form facets which slide against one another within a synovial cavity, the arthrodial membrane having separated into inner and outer lamellae, as at the pivot joints (p. 518). The outer lamella is supported by attenuating zones of red staining cuticle, much as in Iuliformia (compare text-figs 15k with 14b, ventral sides). A very strong yet mobile joint results from these specializations. Manipulation of the skeleton indicates the existence of much greater stability between one segment and the next in the leg of *Polydesmus* than in that of a chilopod.

The manner of evolution of the polydesmoidean type of dorsal hinge is suggested by the condition of the hinge joints of the larger Iuliformia. That of a spirobolid is shown in text-fig. 15m. The hinge is less tight dorsally than in *Schizophyllum* (text-fig. 14a) and the extremity *w* on the femur curls downwards slightly to impinge in a hollow *z* on the postfemur beyond its proximal upcurled margin. An exaggeration of these tendencies could result in the *Polydesmus* condition. A further advancement of this trend is seen in the large *Platyrhacus* where a knob *k.l.* in text-fig. 15l has developed from the region *p.k.* in *Polydesmus* (text-fig. 15k). From this knob levator muscles, *lev.po.fe.* or *lev.ti.* (text-fig. 18j) extend into the proximal segments, a dorsal dilatation making room for the knob. No other example has been found of a hinge joint being provided with a levator muscle. The habits of the large tropical *Platyrhacus* species are not known in detail and their skeletons are heavy (see p. 542).

In *Callipus foetidissimus* the dorsal hinge between tibia and tarsus 1 is much wider than any other hinge, and spreads right across the leg (text-fig. 21e). The tibia bears marked antero- and postero-dorsal sclerotizations, and the wide tarsal sclerotization at the joint is particularly extensive antero-dorsally, so countering forces tending to telescope the leg. This joint in *C. longobardius* and *Polymicrodon polydesmoides* is of the same type although less heavily sclerotized and the amber colour of the tarsal component of *P. longobardius* is antero-dorsal in position. An exaggeration of the antero- and postero-dorsal parts of the articulation could result in a divided hinge such as characterizes the Scutigermorpha (see Part 7). Except for the male *Polymicrodon*, *Callipus foetidissimus* possesses longer legs than any other diplopod so far examined, and this fleet carnivore rapidly changes direction by running in acute hairpin bends in a manner reminiscent of Symphyla. Such behaviour probably has a protective significance in that carnivorous Arachnida cannot change

their direction of running so speedily, but it puts great strains on the tibia-tarsus joint where a great range of flexures take place.

The hinge joint between tarsus and claw is fairly uniform in structure in Chilopoda and Diplopoda. A variety of diplopod claws is shown in text-fig. 16. The cuticle of the distal part of the tarsus is usually thicker dorsally than ventrally, and it enlarges distally to form a concave articular facet across the limb for the proximal dorsal rim of the claw, the arthrodial membrane here being very tight where it forms the dorsal hinge. The claw may be almost or quite solid. Ventrally the long tendinous apodeme leaves the claw, and ample arthrodial membrane allows considerable flexure between tarsus and claw. *Polyxenus* alone shows a swelling on the claw apodeme; this



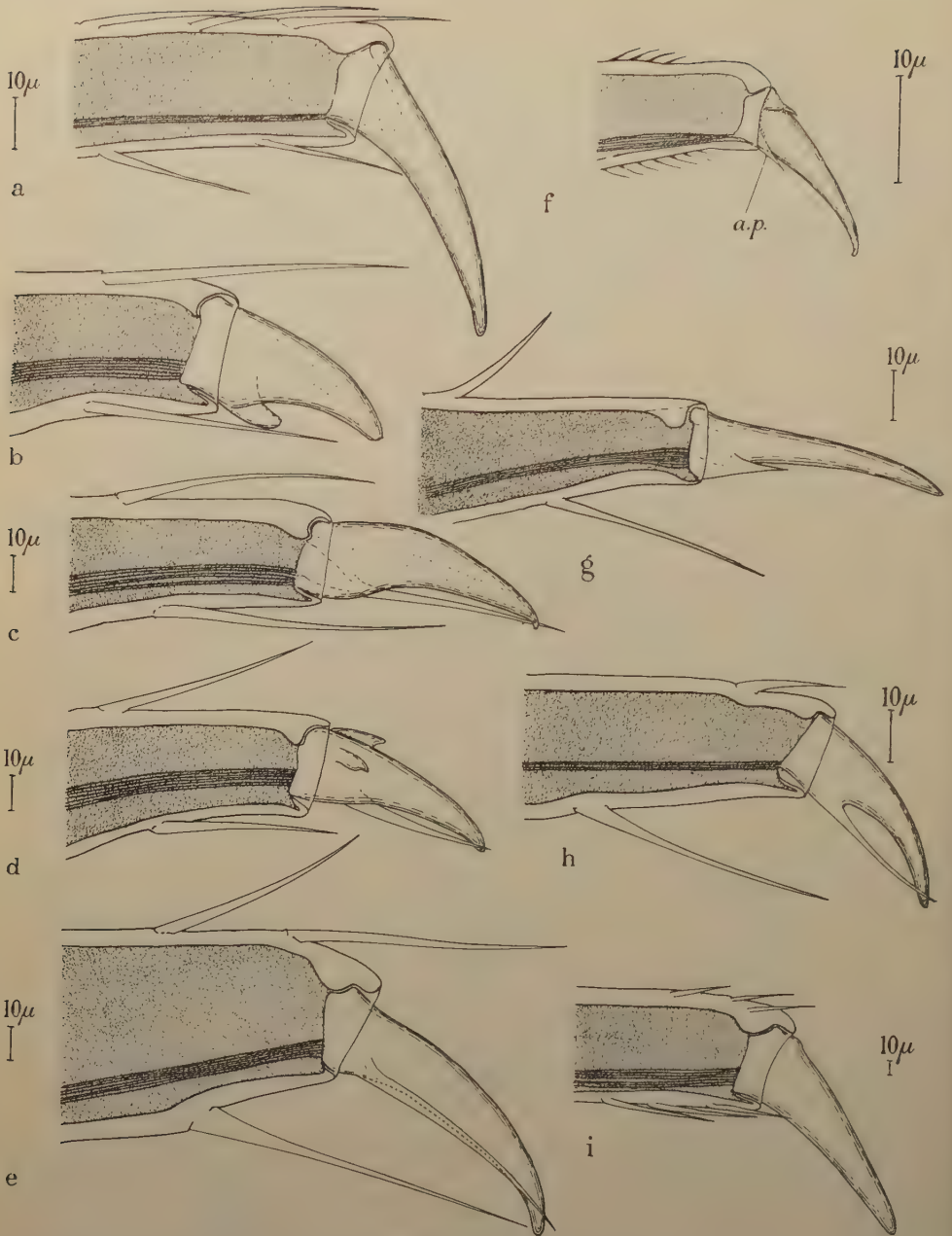
TEXT-FIG. 15.

Hinge joints (cont.).

(k) Joint between femur and postfemur of *Polydesmus angustus*, conventions as in text-fig. 9.

(l) Joint between postfemur and tibia of *Platyrrhacus* sp.

(m) Joint between femur and postfemur of a spirobolid sp.



TEXT-FIG. 16.

Tarsal claws of Diplopoda showing the hinge joint between claw and tarsus. The internal cavity of the distal part of the tarsus is tinted. A $10\ \mu$ scale is shown for each figure, and the length of tarsus is given below for each animal.

length of claw

(a) <i>Polyzonium germanicum</i>	3.1
(b) <i>Lysiopetalum illyricum</i>	Claw worn.
(c) <i>L. illyricum</i>	Claw less worn, 4.3
(d) <i>Polymicrodon polydesmoides</i>	10.1
(e) <i>Tachypodoiulus niger</i>	4.0
(f) <i>Lophoproctus lucidus</i>	9.5
(g) <i>Blaniulus guttulatus</i>	2.1
(h) <i>Cylindroiulus londinensis</i>	4.0
(i) <i>Polydesmus angustus</i>	5.7

lies in the distal part of tarsus 2 (Part 5, text-fig. 4a). Dr. H. Hinton has called my attention to the similarity between this and comparable enlargements on the claw apodemes of some insects from which secretions are poured into the cavity of the apodeme, so causing adhesion of the arolium to the substratum. It is possible that *Polyxenus* produces a similar adhesive secretion.

The claw itself may be quite simple, as in *Polydesmus* (text-fig. 16i) or it may show two types of elaboration. Broadly based subsidiary cusps resembling the main cusp are present in *Polymicrodon*, and in the fast running chilopods such as *Lithobius* and *Cormocephalus*, but not in Geophilomorpha. The subsidiary cusp in chilopods is more ventrally directed than in *Polymicrodon* and arises from the proximal posterior face of the claw. The anterior face of the claw in fleet chilopods may bear a stiff spine such as those on the tarsus. The short dorsal process in *Lophoproctus* (text-fig. 16f) probably represents the larger subsidiary cusp of *Polyxenus* (Part 5, text-fig. 4). Many Diplopoda possess also a thin tapering antero-ventral process from the base of the claw which bends freely; it may be longer than the main cusp and is presumably sensory (text-fig. 16, c, d, e and h and Part 5, text-fig. 4). In the rock-climbing Lysiopetaloida this process and the main claw are often much worn and broken as shown in text-fig. 16b. Where the thin process is very short, as in *Blaniulus* and *Lophoproctus* (text-fig. 16f and g), its function is more problematical, although it may still be sensory. Verhoeff (1927) figures a very large process from the claw of a larval *Schizophyllum*. No animal other than *Polyxenus* possesses an adhesive lappet of partly sclerotized chitin with elastic properties. The claw varies greatly in size relative to the tarsus, being much shorter in *Lophoproctus* and *Polymicrodon* than in other Diplopoda (see legend to text-fig. 16), and is conspicuously long in *Blaniulus* and *Polyzonium*.

LEMB MUSCULATURE OF DIPLOPODA.

The detail of Silvestri's (1903) well illustrated comparative account of diplopod limb musculature has been corroborated for most orders except the Pselaphognatha, in contrast to other existing descriptions and figures which are fragmentary and lack a distinction between the anterior and posterior sides of the leg. In order to appreciate the manner of use of a leg it is essential to know both the exact insertions of all muscles and their positions within the leg. A re-examination of the musculature of limbs in all orders of Diplopoda has been necessary in order to clarify existing accounts, to correct errors, and to provide details where the muscles have hitherto been unknown.

Extrinsic muscles of chilognath Diplopoda.

A minimum of two extrinsic muscles is present in all diplopods, the *protractor coxae* and *retractor coxae* causing the forward and backward swing of the leg. The retractor is always the larger, and usually is inserted on the posterior side of the coxa near the middle line while the protractor inserts antero-laterally (text-figs 4a and b). These positions of insertion are mechanically suitable for both types of coxal swing. The muscles arise from the tracheal pouch of the same side of the body in Colobognatha, Iuliformia and Oniscomorpha. In the Iuliformia, the strength of the leg swing is provided by a very wide retractor coxae fanning over the entire margin of the tracheal pouch, and its tendon runs into the muscle for a considerable distance, so carrying a maximum number of short muscle fibres. The protractor coxae is much narrower. Strong burrowers would be expected to have a retractor muscle with a maximum transverse sectional area, while a weaker protractor suffices to move the leg forwards (p. 499).

In the fleeter diplopods a speedy and large displacement at the coxal articulation is required to give the shorter pace durations (Part 4, p. 336) and longer strides. The Polydesmoidea (Part 4, text-fig. 3e and f) and Nematophora (text-figs 5f and

g and 19-21) possess the normal pair of extrinsic muscles, the *protractor brevis coxae*, *pr.co.b.* and *retractor brevis coxae*, *ret.co.b.*, coming from the tracheal pouch of the same side. But in addition a *protractor longus coxae*, *pr.co.l.* and *retractor longus coxae*, *ret.co.l.* come from a tracheal pouch of the opposite side. In the Nematophora the protractor longus coxae arise from the opposite tracheal pouch of the preceding segment, thereby avoiding mechanical interference with the tracheal pouch of its own segment. Nematophoran diplosegments are shorter than are those of Polydesmoidea, and a working model demonstrates the impossibility of the protractor longus coxae being attached to the skeleton of the same segment.

The wide retractor brevis coxae of *Polydesmus* (Part 4, text-fig. 3e) fans out to a maximum, and its large sectional area doubtless provides strength for this type of leg as in Iuliformia. This muscle in *Microchordeuma* is about half the length of the retractor longus, a little less in *Polymicrodon*, and only a quarter of the length of the longus muscle in *Callipus* (text-figs 19-21, *ret.co.b.* and *ret.co.l.*). The longus muscles also are relatively longer in *Callipus* than in the other two animals, although the leg length of *Callipus* is equivalent to that of *Polymicrodon*. Since *Callipus* executes more rapid but weaker leg movements than the Chordeumoidea (p. 490), it may be suggested that the brevis muscles mainly provide strength to the leg movement here, as in Iuliformia, while the longus muscles provide displacement at the joint and therefore long strides and speed. The distance between the points of origin of the retractors and protractors on the coxa is much less in *Callipus* than in the Chordeumoidea; where this distance is small the displacement of the distal end of the coxa will be greater for the same amount of shortening of the longus muscles. *Polymicrodon* would therefore be expected to exert stronger leg movements than *Callipus* but to take smaller strides, as in fact it does.

The great fleetness of the Lysipetaloidea is clearly due to the narrow coxal base, to a reduction in size of the extrinsic brevis muscles together with an increase in length of the extrinsic longus muscles and of the tracheal pouches to which they are attached. The slender longus muscles of the Polydesmoidea probably contribute to the fairly long strides when running, while the short wide brevis muscles provide the strength of the pushing movements in woodland litter.

Three further extrinsic leg muscles are present in some diplopods. The *retractor prefemoris* of the Oniscomorpha (text-fig. 4d, *ret.p.fe.*) represents the more dorsal section of the normal diplopod depressor prefemoris which has shifted its origin from the coxa to the tracheal pouch, doubtless in association with the weakness of the coxa-body articulation. The *levator prefemoris* is similarly divided, the usual muscle being represented by levator prefemoris internus, *lev.p.fe.int.*, its dorsal sector *lev.p.fe.* arising from the tracheal pouch.

An extrinsic levator prefemoris is present in Colobognatha and Polydesmoidea. In *Polyzonium* it arises from the tracheal pouch not far from the spiracle and close to the origin of the retractor to the coxal sac (text-fig. 4b). This muscle appears to be intrinsic in *Pseudodesmus* (Silvestri, 1903, fig. 32b). In the Polydesmoidea levator femoris arises from the inner ramus of the tracheal pouch of the same side close to the ventral ectoderm (text-fig. 5h and Part 4, text-fig. 3e, *lev.p.fe.*), and is a much longer muscle than that of *Polyzonium*. Extrinsic levators are all concerned with the problem of the initial upward bend of the leg (pp. 501, 505, 507). The width of the coxal base in the Oniscomorpha and *Polyzonium* provides space for an extrinsic levator, while there could be no such muscle passing through a coxa shaped as in the Iuliformia. In the Polydesmoidea the chilopod-like position of origin of the leg allows a larger displacement between the coxa and prefemur (text-fig. 5h and 12), and if this is to be implemented a sufficiently long levator muscle must be present. The presence of a long extrinsic levator prefemoris muscle in Polydesmoidea and a similar levator trochanteris muscle in Chilopoda (text-fig. 6) represents a striking functional convergence. Such a muscle is mechanically impossible to a nematophoran, and long intrinsic levators are developed instead (p. 533).

All Nematophora possess a *rotator trochanteris* muscle (*r.tr.* text-figs 19–21, and Silvestri, 1903, fig. 328 *d*, *m.longus anuli subcoxalis*), arising from the tracheal pouch just lateral to the brevis muscles and passing as a long narrow double strand to the posterior edge of the trochanter between its ventral margin and the level of the pivot joint. No actual rotation can be produced by this muscle because of the nature of the coxa-trochanter pivot joint, but the mobile trochanter will be braced against the pull exerted by the longus muscles from the tarsus or tibia which are inserted on the proximal posterior margin of the trochanter just above the rotator trochanteris. No other diplopods possess any of these muscles, all of which are concerned with fleetness.

Intrinsic muscles of chilognath Diplopoda.

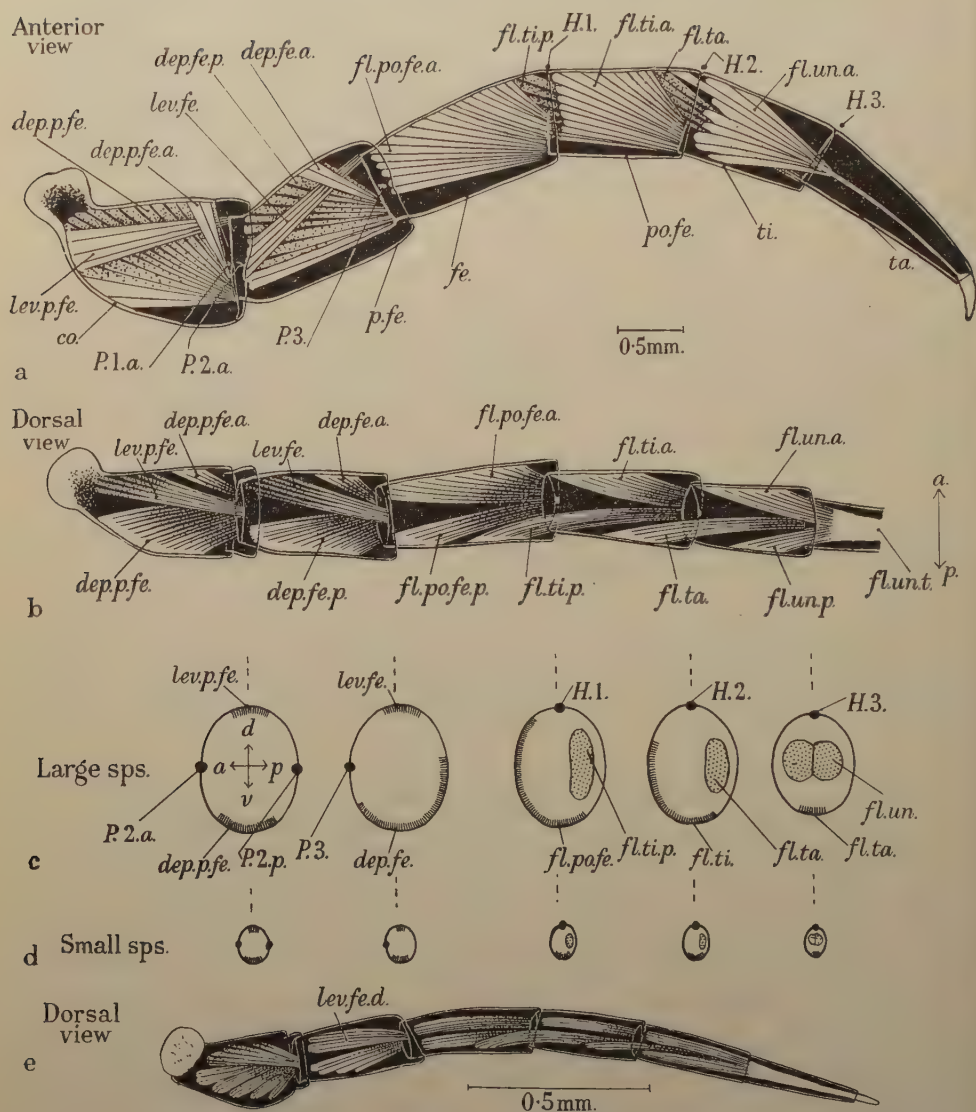
The simplest arrangement of muscles is found in the smaller Iuliformia, and variations of the same plan occur in the Colobognatha, Oniscomorpha and Polydesmoidea. Basically the Diplopoda are adapted for strong pushing by the legs (Part 4), and many short intrinsic muscles are usual in all groups except those in which pushing has been abandoned in favour of fleetness (p. 499), the Nematophora and Pselaphognatha showing the greatest divergence from the common plan.

Basic plan of limb musculature. Text-fig. 17 presents the arrangement of muscles in large and small species of typical Iuliformia. The smaller legs possess fewer muscle bundles than the larger, and increase in size of the leg is associated with more extensive muscle insertions and an increase in muscle complexity resulting in a greater transverse sectional area of muscle.

Crossed *levator prefemoris* and *depressor prefemoris* muscles arise on the anterior and posterior faces of the coxa respectively, the depressor being the bulkier of the two. In large species there may be room for an anterior section of the depressor, *dep.p.fe.a.*, text-fig. 17*a* and *b*, without causing mechanical interference with the levator.

A similar pair of crossed *levator femoris* and *depressor femoris* muscles lie anteriorly and posteriorly respectively in the prefemur. The levator is much the smaller and usually arises near the anterior proximal edge of the prefemur opposite pivot joint *P.2*, and the whole lower sector of the prefemur may be occupied by the depressor. In *Schizophyllum* the levator is entirely dorsal and anterior in position while the depressor lies in the posterior half of the leg, text-fig 17*e*. In large species the insertion of the depressor spreads from the mid-ventral position along the posterior margin of the femur as far as space allows, and an anterior strand *dep.fe.a.* is present when there is sufficient space for it, text-fig. 17*a* and *b*.

Flexors only are present beyond the pivot joints. They form two series lying on the anterior and posterior sides of the leg, inserting mid-ventrally on the proximal ends of the segments or on the claw apodeme (text-fig. 17*a*, *b* and *e*). The anterior components of *flexor postfemoris* and *flexor tibiae* cross one joint only and arise from the proximal dorsal ends of the femur and postfemur respectively in small species, and from the whole length of these segments in large ones. The *posterior component* of *flexor postfemoris* arises from the proximal end or proximal half of the femur in small and large species respectively, the prefemur-femur joint preventing any further proximal extension of the muscle. The *posterior component* of *flexor tibiae* and the whole of *flexor tarsi* cross two joints, and arise from the middle or distal halves of the femur and tibia respectively. The *anterior component* of *flexor unguiculi* arises from the proximal end or from the whole of the tibia, sometimes extending just into the postfemur (text-fig. 17*a*), while the *posterior component* is usually a little shorter than the anterior, having to avoid mechanical interference with flexor tarsi. In large species the insertions of flexores post-femoris and tibiae may spread up the anterior proximal margins of the postfemur and tibia as far as space permits (text-fig.



TEXT-FIG. 17.

Typical limb musculature of large and small species of Iuliformia. All spines are omitted. See also text-fig. 4a.

- (a) Anterior view of leg of large spirobolid sp. Similar muscles are present in large Spirostreptomorpha.
- (b) Dorsal view of the same.
- (c) Transverse views of anterior ends of prefemur, femur, postfemur, tibia and tarsus to show positions of origins of main muscles in the larger species of Iuliformia.
- (d) Transverse sections corresponding to the above to show origins of main muscles in small species of Iuliformia.
- (e) Dorsal view of the leg of *Schizophyllum sabulosum* to contrast with fig. b.

17c); no posterior spread is possible because it would lead to mechanical interference with the posterior components of the flexors.

The greater length of the posterior compared with the anterior components of the flexor muscles must tend to give greater displacement on the posterior side of the joints than on the anterior during the backstroke. This effect will brace the leg against the force exerted by the extrinsic retractor which tends to produce an anterior concavity along the leg. The posterior flexors may also produce slight bending of the leg in the opposite direction in fleeter species which, as shown in text-fig. 3d, will tend to increase the stride; emarginations of the leg segments facilitate these bends (p. 507). In large species the posterior spread of the insertion of the depressor femoris must provide a useful retractor as well as depressor force, the anterior strands *dep.fe.a.* giving a compensating stability to the joint. The spreading insertions of the flexor muscles on the proximal ends of postfemur and tibia represent the only way in which the bulk of the muscle can be increased in large species without causing mechanical interference.

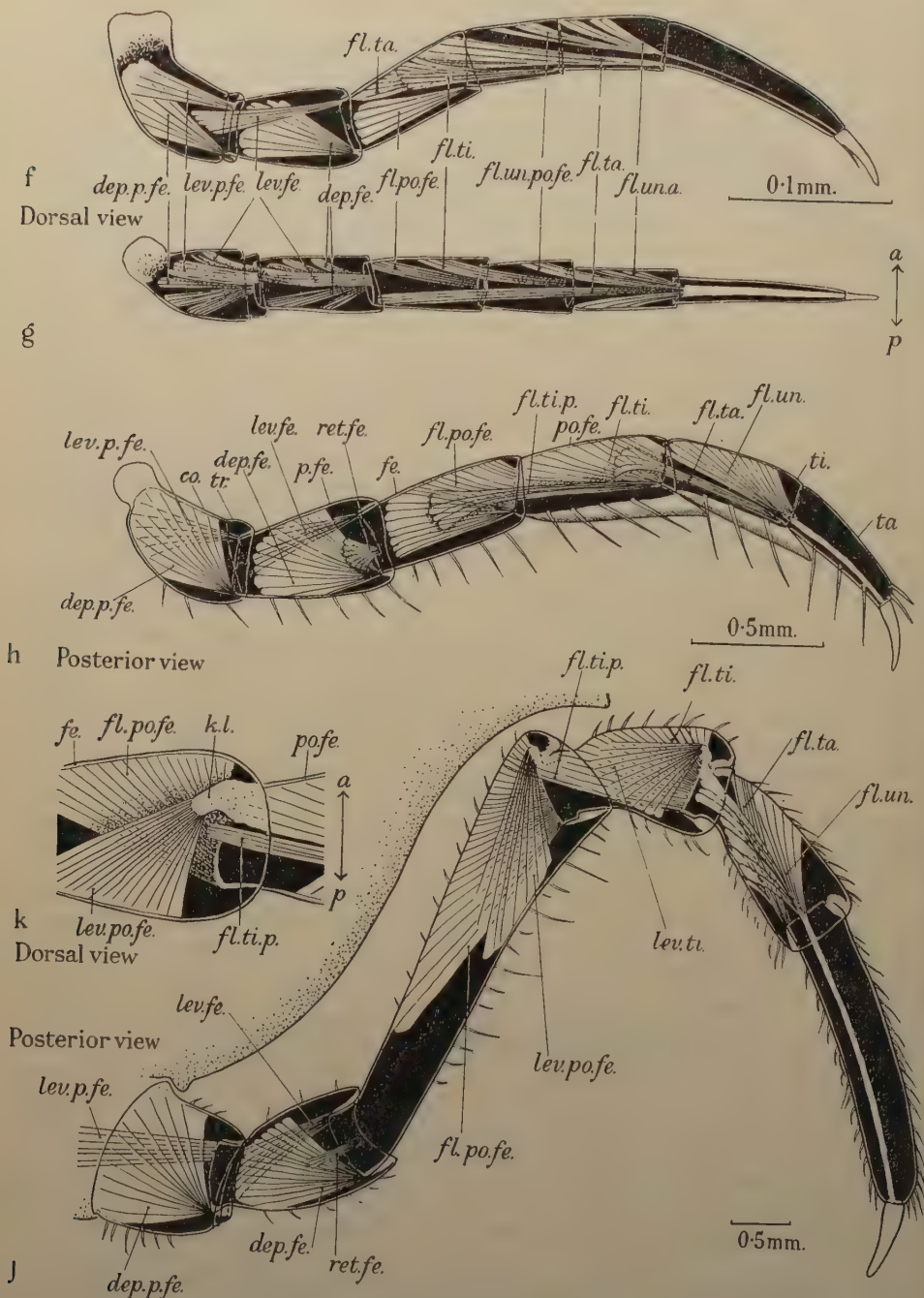
The anterior distal emargination of the prefemur (text-fig. 17b and e, and (p. 507) may cause slight promotion of the femur when levator femoris contracts, the posterior pivot joint components opening out. In the smaller Iuliformia and Oniscomorpha such movement if any is slight. In larger Iuliformia, in Colobognatha, Polydesmoidea and Nematophora a *retractor femoris* controls this movement, and a comparable control is exercised also by the *retractor prefemoris* in Colobognatha (text-figs 4b, 5h, 12, 18h and j and 21a). The need for these muscles appears to be associated with limb movements requiring great precision, as in *Polyzonium* progressing across a chalk ceiling, or with strong movements as in Polydesmoidea, or with large angles of leg swing and fleetness as in Lysiopetaloidea, or simply with size as in large Iuliformia. The retractor prefemoris of *Polyzonium* arises from the posterior proximal margin of the coxa and inserts widely on the posterior rim of the prefemur, level with the large anterior pivot joint components, the posterior components are very small, if present at all (the level of the pivot is shown by the black dot on the left side of text-fig. 4b and the muscle is drawn on the right leg). In the larger Iuliformia and in Polydesmoidea and Colobognatha a short retractor femoris arises from the posterior distal face of the prefemur and inserts on the well-formed posterior femoral component of the pivot joint in the two former groups (text-figs 4b, 5h, 18h and j), appearing to be more tendinous than muscular in *Platyrhacus*.

Limb musculature of Nematophora. The basic plan of muscles just described is recognizable in the Nematophora (text-figs 19–21), but is much changed in association with the fleetness obtained by quicker stepping and the use of a large angle of swing (p. 493). The development of two systems of long intrinsic muscles, levators to the femur and flexors to the distal part of the leg, achieves the necessary increase in displacement at the joints and the quicker stepping (p. 499) and is responsible for many harmonious alterations in other muscles.

The *levator femoris longus* is entirely dorsal, as is the levator femoris of *Schizophyllum* with which it is doubtless homologous (text-fig. 17e). The levator femoris longus of Nematophora arises on the dorsal face of the coxa *lev.fe.l.*, with a section coming from the anterior coxal face, *lev.fe.l.a.* in *Polymicrodon* and *Callipus*. In the Chordeumoidea a part of this muscle inserts some distance along the femur, as shown in text-figs 19 and 20, *lev.fe.l.d.* Contraction of this system will telescope the coxa-trochanter, the trochanter-prefemur and the prefemur-femur joints giving maximum levation.

The development of the long levator system has either necessitated or permitted alterations in other muscles within the coxa and prefemur. The normal mid-dorsal insertion of levator prefemoris has shifted posteriorly (text-figs 17 and 21b), so making room for the long levator and, unlike all other diplopods, levator prefemoris here arises on the posterior instead of the anterior face of the coxa. This change in origin

Anterior view



TEXT-FIG. 18.

Limb musculature (cont.).

(f) and (g) Anterior and dorsal views respectively of the leg of *Blaniulus guttulatus*, all spines omitted.

(h) Posterior view of the leg of male *Phasioporus salvadorii*.

(j) Posterior view of the polydesmiodean *Platyrhacus* sp.

(k) Dorsal view of distal end of femur of *Platyrhacus* sp.

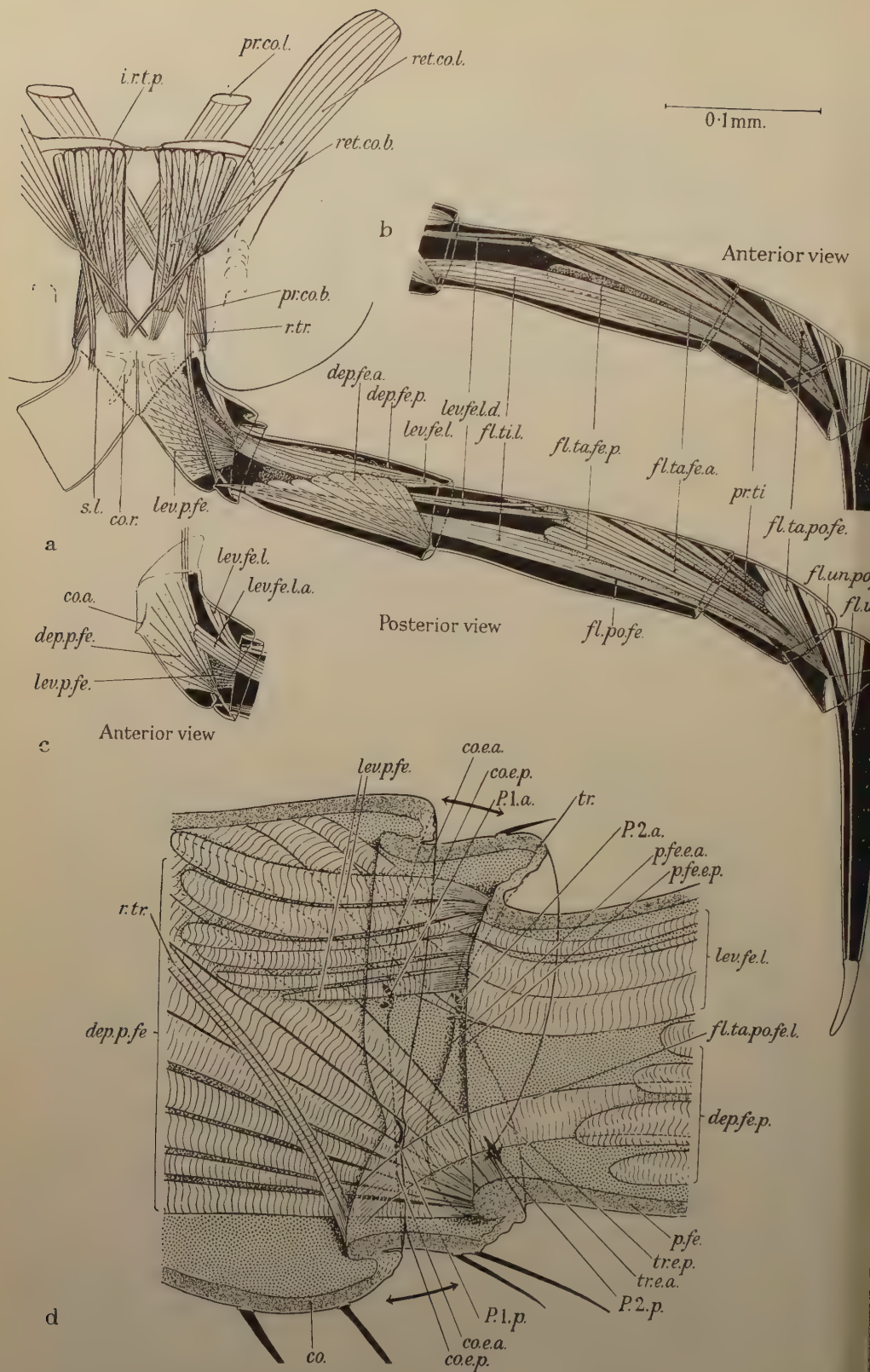
gives a levator force balancing that of *lev.fe.l.a.* The depressor prefemoris is as large as is mechanically possible; it fills the whole coxa and arises mainly from its mesial and anterior faces. The dorsal position of levator femoris longus frees the whole anterior face of the prefemur, and very large anterior and posterior components of depressor femoris *dep.fe.a.* and *dep.fe.p.* fan out over the anterior and posterior faces of the femur; other diplopods only possess a very small anterior component or none at all (text-fig. 17a and e).

Coxal sacs, present in the anterior legs of the Lysiopetaloidea, possess no rigid framework as seen in those of the Colobognatha, and consequently retract much flatter within the leg, causing no disturbance of the muscles within the coxa. The retracted sac lies posterior to depressor prefemoris, as in *Polyzonium*.

The distal flexors of the leg differ conspicuously from other diplopods in the presence of a very long muscle arising on the proximal postero-ventral rim of the trochanter and inserting mid-ventrally on the tibia in Chordeumoidea and on the tarsus in Lysiopetaloidea (*fl.til.* and *fl.ta.l.*), and uniting with a small flexor postfemoris in the proximal part of the femur. It is probable that these longus muscles are of the greatest importance in providing large and speedy displacements (p. 499). They are clearly homologous in Chordeumoidea and Lysiopetaloidea although extending one segment further down the leg in the latter. This condition may have arisen from that of the Chordeumoidea by the union of a flexor longus tibiae with a normal flexor tarsi. The tibia would thus be left with no ventral flexor, as in text-fig. 21a, a unique condition in diplopods and an indication of the highly specialized condition of the Lysiopetaloidea. Diagnoses of the flexor muscles of Chordeumoidea and Lysiopetaloidea are given in Table II, the differences probably indicate divergent paths of evolution. The Chordeumoidea show considerable elongation of the components of flexor tarsi while the flexor tarsi longus of the Lysiopetaloidea is associated with the smaller femoral component *fl.ta.fe.*, text-fig. 21. The large component of flexor tibiae arising from the femur in *Polymicrodon* only is probably associated with pushing by the dorsal surface and pulling the legs well under cover of the keels.

The contraction of longus muscles causing telescoping of joints where no direct muscles are involved is rare in diplopods; longus muscles do not appear to be primitive features but specializations correlated with long strides and large displacements at the joints. The postfemur-tibia joint of *Callipus* is moved by flexor tarsi longus and both coxa-trochanter and trochanter-prefemur joints of all Nematophora are telescoped by levator femoris longus. The incomplete joint between tarsus 1 and tarsus 2 is also flexed indirectly by flexor unguiculi, but here the joint is clearly a later evolution than the long apodeme from the claw, and the absence of direct flexor muscles to tarsus 2 appears to be primitive and not a secondary condition. The ventral flexures about the trochanter (text-fig. 19d) effected by the crossed depressor prefemoris and flexor tarsi postfemoris longus are unique in diplopods. Each muscle tends to move two joints, and the origin of the longus muscle from the trochanter and not from the proximal part of the prefemur may give some resilience to the movements comparable to the suggested (p. 522) elastic properties of the chilopod trochanter.

Protractors of the postfemur and tibia are present in the Nematophora and are most fully developed in the Lysiopetaloidea. A more extensive series of protractors occurs in Chilopoda, and such muscles are lacking in other chilognath Diplopoda. Protractors thus characterize the fleetest faster-stepping animals and presumably serve two functions. The leg segments of these animals are more loosely articulated than in burrowing forms, so allowing a wider range of displacements at the joints, and the longus flexor muscles and the long posterior components of flexors tend to produce a retractor movement owing to the emarginations of the segments. This retraction is antagonized by the protractors which can either maintain the straightness of the leg, or produce a slight forward bending along the leg during the forward stroke and so contribute to stride length. *Microchordeuma*, with a shorter leg than *Poly-microdon* and *Callipus* has only a protractor tibiae arising from the distal dorsal half



TEXT-FIG. 19.

TABLE II

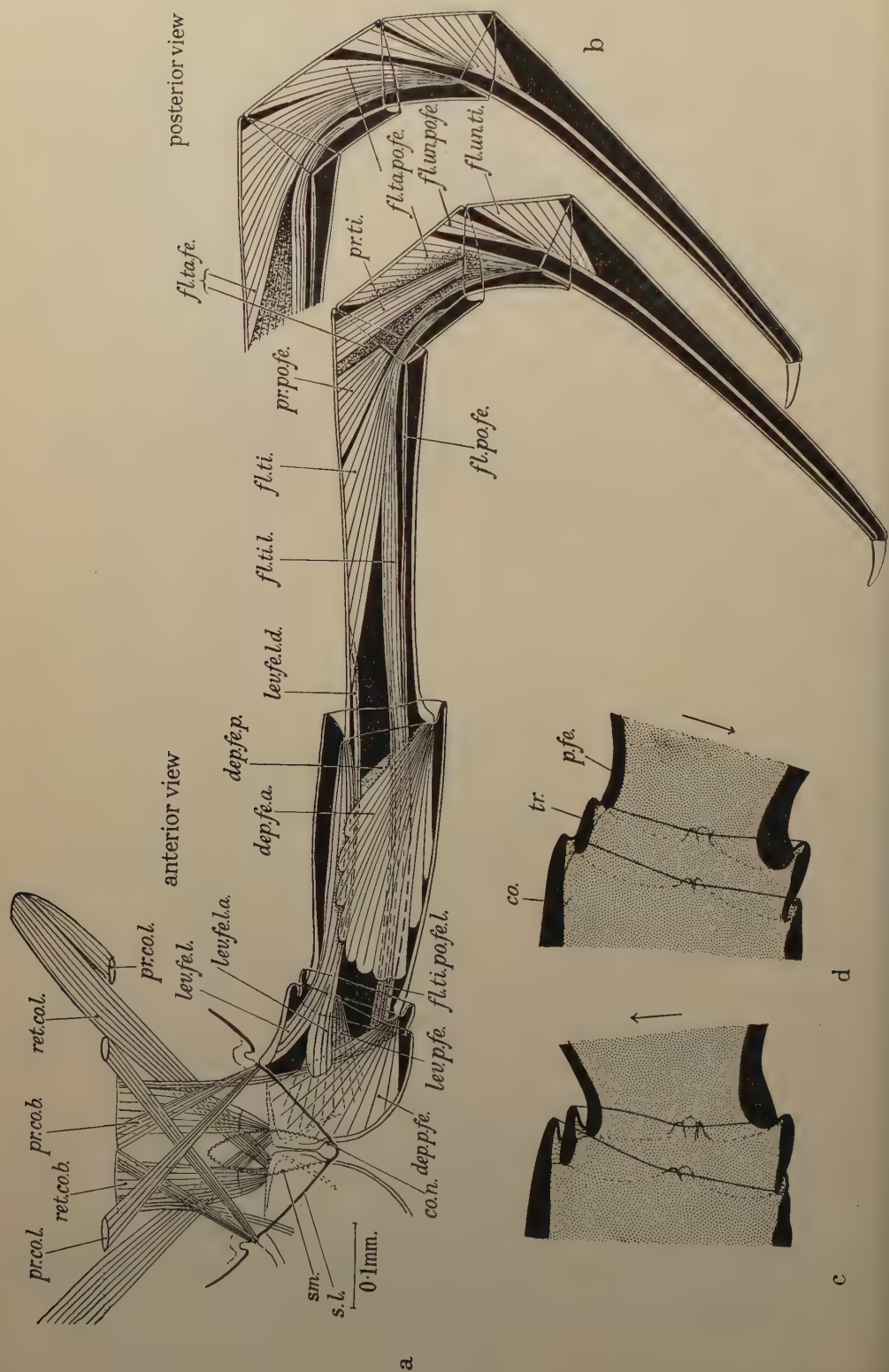
<i>Microchordeuma scutellare</i>	<i>Polymicrodon polydesmoides</i>	<i>Callipus and Lysiopetalum</i> sps.
<i>flexor postfemoris. fl.po.fe.</i> From : proximal ventral margin of postfemur, a small strand. To : join main flexor longus muscle complex (<i>fl.ti.l.</i> or <i>fl.ta.l.</i>)		
<i>flexor tibiae</i> Absent.	<i>flexor tibiae. fl.ti.</i> From : tendon on proximal ventral margin of tibia. To : proximal 2/3 of dorsal face of femur.	Absent.
<i>flexor tibiae longus. fl.ti.l.</i> From : tendon on proximal ventral margin of tibia. To : postero-ventral proximal margin of trochanter.		
<i>flexor tarsi</i> From : proximal ventral margin of tarsus or from a long tendon arising in this place in <i>Lysiopetaloides</i> .		
<i>flexor tarsi longus</i> represented by <i>fl.ti.l.</i>		<i>flexor tarsi longus fl.ta.l.</i> To : postero-ventral proximal margin of trochanter.
<i>fl.ta.fe.p.</i> To : postero-dorsal face of femur.	Absent.	Absent.
<i>fl.ta.fe.a.</i> To : antero-dorsal face of middle of femur, longer than <i>fl.ta.fe.p.</i>	<i>fl.ta.fe.</i> To : dorsal face of distal half of femur.	<i>fl.ta.fe.</i> To : distal dorsal face of femur, small in extent.
<i>fl.ta.po.fe.</i> To : postero-dorsal face of middle of postfemur.	<i>fl.ta.po.fe.</i> To : proximal 2/3 of postero-dorsal face of postfemur.	
<i>flexor unguiculi</i> From : apodeme of claw in proximal part of tarsus, passing in several sections.		
<i>fl.un.po.fe.</i> To : distal dorsal face of postfemur.	<i>fl.un.po.fe.</i> To : distal dorsal face of postfemur, small in extent.	<i>fl.un.po.fe.</i> To : antero-dorsal face of postfemur.
<i>fl.un.ti.</i> To : proximal dorsal face of tibia.	<i>fl.un.ti.</i> To : whole of dorsal face of tibia.	<i>fl.un.ti.</i> To : whole postero-dorsal face of tibia.

Table showing component parts of the flexor muscles from the postfemur, tibia, tarsus and tarsal claw in Nematophora. The abbreviations are those used in text-figs 19-21.

TEXT-FIG. 19.

Text-figs 19-21 show the limbs and musculature of Nematophora. The limbs articulated to the sternites are slightly tilted, so that the proximal segments of the leg in posterior views are slightly postero-dorsal in aspect, and in anterior view are a little antero-ventral. The shafts of the longus muscles are more complex than shown.

- (a) to (c) *Microchordeuma scutellare*. (a) Posterior view, (b) anterior view, (c) anterior face of coxa and trochanter.
- (d) Postero-dorsal view of trochanter of *Callipus longobardius* to show its associated muscles and articulation. The arrows indicate the maximum possible displacement of the rigid part of the coxa relative to the trochanter. The anterior pivoting articulations *P.1.a.* and *P.2.a.* and the anterior segment boundaries are shown by dotted lines.



of the femur, which doubtless tends to protract both postfemur and tibia. *Poly-microdon* possesses separate protractors to the postfemur and tibia, the former being short, and both arise distally on the dorsal face of the femur. The *Lysiopetaloides* have much longer protractors to the postfemur and tibia, arising over the whole postero-dorsal face of the femur. Their greater length is associated with the corresponding greater length of flexor tarsi longus.

Thus the differences between the basic plan of diplopod limb muscles and the muscles present in the *Lysiopetaloides* indicate that the evolution of long levator and long flexor muscles and the presence of protractor muscles is associated with long strides and fast stepping, in contrast to the short muscles found in strong burrowers. Some specializations found in the musculature of certain chilognath Diplopoda may now be considered.

Specializations of the Colobognatha: Polyzonium. The basic plan of the limb muscles resembles that of the *Iuliformia*, but modifications are present proximally in association with mechanical interference by the large and rigid coxal sac in almost every leg, and by the difficulty of the initial part of the S-shaped bend. The anterior face of the coxa is not occupied by the levator prefemoris, as in other diplopods, the levator having become extrinsic (p. 530); the whole of this region houses a very wide depressor prefemoris, a unique condition among diplopods, and doubtless due to the coxal sac and its retractor muscles occupying the posterior part of the coxa. The retractor prefemoris takes part of the space normally used by the depressor prefemoris. Levator femoris is in two parts, the normal muscle arises antero-ventrally in the prefemur, while a longus muscle arises on the anterior face of the coxa (text-fig. 4b left side, *lev.fe.* and *lev.fe.l.*; only part of *lev.fe.l.* is shown on the right). Thus the proximal limb muscles of *Polyzonium* show specializations correlated with the habit of clinging closely to chalk faces, in contrast to the many primitive features possessed by the order.

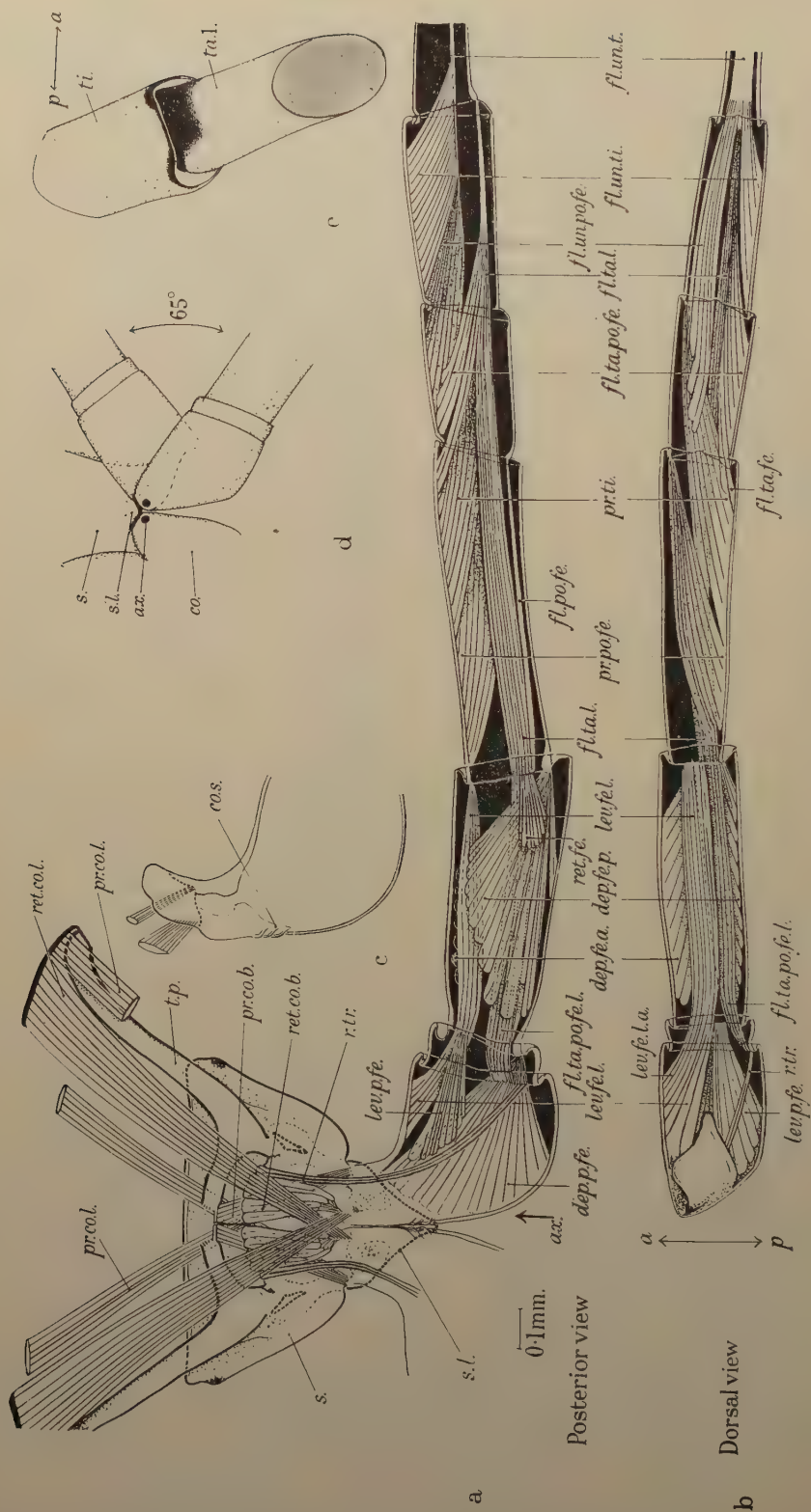
Specializations of the Iuliformia: Plusioporus. Some *Iuliformia* tend to run a little faster and to live more exposed lives than the predominant burrowers. The leg of *Plusioporus salvadorii* (text-fig. 18h) possesses not only a retractor femoris but flexor tarsi and the posterior component of flexor tibiae arise well down the posterior faces of the femur and postfemur, instead of nearer to the dorsal surface, and must give a strong retractor force. These muscles may be of service when burrowing into loose mould. *Plusioporus sulcatus* rapidly burrows into such material which is easily shifted, and the stepping then becomes almost a rowing movement for which retractors are appropriate. Whether the ventral flanges projecting from the postfemur and tibia which increase the blade of the limb facilitate such movements is unknown. These flanges are only present in males; the blunt ventral margins are finely serrated and perhaps assist in gripping the females.

Specializations of the Iuliformia: Blaniulus. The legs of *Blaniulus* differ from other *Iuliformia* in the greater length of the tarsus and tarsal claw, and of the levator and flexor muscles (text-fig. 18f and g). These features suggest that the leg cannot give such strong movements but might give greater displacements at the joints or more speedy movements. It has been shown that a leg of *Blaniulus* does not exert so strong a force as a normal iuliform leg of comparable size would do (Part 4, pp. 342, 345), and it has been suggested that these animals do not push

TEXT-FIG. 20.

Nematophoran limbs (cont.).

Poly-microdon polydesmoides. (a) Anterior view, (b) posterior view, (c) and (d) diagrams showing the form of the trochanter and the displacements of the trochanter and prefemur when the distal part of the leg is elevated (c) and depressed (d).



TEXT-FIG. 21.

their way through soil to the same extent as other diplopods, but instead twist and turn to use small existing spaces. *Blaniulus* is not fleet, although it can walk a little faster than a normal iuliform of comparable size, and its legs are a little shorter than are those of most Iuliformia (Part 4, Table I), thereby gaining sufficient cover from the narrower rings.

Photographs of the animals in ventral view show that the legs can swing through 83° during the backstroke (Pl. 9, fig. 22), a much larger angle than that of other Iuliformia, and exceeded only by the Lysiopetaloidea. The longer diplosegments make room for such a swing, and the long intrinsic muscles provide the larger joint displacements needed to give so large an angle, although they do not provide quicker stepping. Leg morphology is thus in keeping with the performance of the leg.

Levator femoris arises on the anterior face of the coxa, passing to the side of levator prefemoris. Anterior components of depressor femoris arise from the anterior face of the prefemur, space being available owing to the position of origin of levator femoris. This unusual condition in so small a leg may be associated with the very marked anterior emargination of the prefemur, facilitating promotion on the forward stroke, the anterior component of depressor femoris protracting the femur. The anterior component of flexor tibiae arises from the distal half of the femur instead of from the postfemur, and an anterior component of flexor unguiculi arises from much of the postfemur in contrast to its origin in text-fig. 17*b* and *e*. The posterior side of the distal segments is occupied by a very long flexor tarsi arising from the anterior end of the femur. This muscle telescopes the femur-postfemur and postfemur-tibia joints which have no posterior flexors of their own in a manner comparable to that of the Lysiopetaloidea.

Specializations of the Polydesmoidea: Polydesmus and Platyrrhacus. The legs of the Polydesmoidea are stronger than those of all other Diplopoda (Part 4, pp. 338 and 340) and might be expected to show structural differences from other diplopods. The extrinsic origin of levator prefemoris (p. 530) frees the anterior face of the coxa, so that it becomes possible for the depressor prefemoris to arise from the entire proximal margin of the coxa (see transverse section on the left of text-fig. 5*h*), the muscle thereby becoming about twice as extensive as in a typical diplopod where the levator lies in the anterior and the depressor in the posterior part of the coxa. A maximum depressor force can thus be exerted on the prefemur. The dorsal dilatation of the prefemur makes space for a very wide depressor femoris whose large transverse sectional area must contribute great strength to the leg.

The arrangement of the flexor muscles in *Polydesmus* and *Platyrrhacus* (text-figs 5*h* and 18*j*) is very similar to that of the Iuliformia, except that the dorsal dilatations of the postfemur and femur make space for an anterior extension of the insertions of flexores postfemoris and tibiae along the proximal rims of the postfemur and tibia right up to the dorsal hinge, so increasing the number of muscle bundles and therefore the strength of leg movements. The anterior fibres of the flexors are longer and more numerous in the larger *Platyrrhacus* than in *Polydesmus*, Silvestri (1903) called them protractors in *Platyrrhacus*, but did not record them for other genera. The joints appear to be too rigidly articulated to allow any protractor movements, and the extension of the flexor muscles along the anterior rims of the postfemur and tibia exactly parallels the similar spread in larger Iuliformia (text-fig. 17*a* and *c*), and is

TEXT-FIG. 21.

Nematophoran limbs (*cont.*).

- Callipus longobardius* (a) to (d). (a) Posterior view, (b) dorsal view, (c) base of coxa showing articulating folds, *co.s.*, (d) diagram showing a 65° rotation of the coxa about its almost vertical axis, "*ax*".
- (e) Postero-dorsal view of hinge joint between tibia and tarsus 1 of *Callipus foetidissimus*, heavy sclerotization being shown in black.

probably correlated with size and strength of the leg and not with promotion. The apparent curvatures of the legs in Part 4, Pl. 55, figs 38–41 is due to foreshortening.

The legs of the large tropical *Platyrrhacus* (text-fig. 18j) are heavily built and appear to be even more suited to dorsal pushing than are those of *Polydesmus*. The prefemur is shorter and the femur longer than in *Polydesmus* (text-fig. 5h) and the femur, postfemur and tibia house a maximum of short muscles, the proximal part of the femur being devoid of musculature, as in no other diplopod so far seen. Distal dorsal dilatations of the femur and postfemur are more marked than in *Polydesmus*, and the most dorsal parts of the anterior flexores postfemoris and tibiae run dorso-ventrally from the dilatations.

The most remarkable feature of the leg of *Platyrrhacus* is the presence of levator muscles to the postfemur and tibia, no such muscles being present in other Diplopoda. The flexor muscles within the postfemur and tibia occupy the anterior half of the leg, flexor tarsi and the usual posterior component of flexor tibiae arising dorsally and not postero-dorsally as in most Diplopoda. The posterior half of the leg houses levator muscles. A forward extension of the cuticle from the region marked *p.k.* on text-fig. 15k below the dorsal hinge of *Polydesmus* could give a strong antero-dorsal apodeme on to which levator muscles could be attached as in *Platyrrhacus* (*k.l.* in text-figs 15l and 18k and j). The length of the apodeme is sufficient to give a lever action whereby a muscle very close to the hinge can be effective. These posterior levators contrast in position with the levator muscles in more proximal leg segments which are predominantly antero-dorsal in position. Levator muscles are usually of importance during the forward stroke, and tend to produce slight promotion also, and they are usually much weaker muscles than the corresponding depressors or retractors (text-figs 17 and 18). Levator postfemoris and levator tibiae of *Platyrrhacus* on the contrary are very wide muscles and clearly strong in contrast to levator femoris. It may be suggested that these levators are used during the backstroke when the animal is pushing with the dorsal surface. If the leg were flexed much as in text-fig. 18j, contraction of depressor prefemoris, depressor femoris, levator postfemoris and levator tibiae would all tend to straighten the leg and raise the animal from the ground. *Polydesmus* already has a maximum development of the two proximal depressor muscles, and with increase in size of an animal of this type weaker pushing by the dorsal surface and keels would result, unless extra musculature could be contrived, and the unique levators to the postfemur and tibia appear to be the solution of the problem of maintaining pushing power with increase in size. The animal has not been seen alive, but the great rigidity of the cuticle and joints as well as the musculature suggest that strong movements characterize *Platyrrhacus*.

Thus the specializations which exist throughout the legs of Polydesmoidea are all concerned with the production of strong movements by muscles which possess the greatest transverse sectional area.

Limb skeleton, musculature and movements in Pselaphognatha.

Polyxenus is too small and spinous for direct observation of details of leg movement, but much can be deduced from comparative morphology of cuticle and muscles and photographic evidence of the range of leg swing. *Polyxenus* steps more rapidly than all chilognath Diplopoda other than Lysioptaloidea, and the short legs move through as large an angle of swing as is found in Chilopoda and Lysioptaloidea (Table I, p. 495). The leg musculature is described in Part 5 and limb skeleton in Part 5 and above (p. 522), but the significance of the details of neither could be apprehended until the work for Parts 6 and 7 had been completed.

That the leg of *Polyxenus* can only serve weak movements and not strong ones is suggested by:—the great mobility of the trochanter; the evolution of a chilopod-like Y-skeleton from the anterior components of the three typical diplopodan pivot joints, so forming the weak but mobile anterior coxa-prefemur hinge (p. 522); the

type of leg swing (p. 496 and 498); the stance (p. 501) and the long divided tarsus (p. 503). The musculature has departed considerably from the basic diplopodan plan (summarized on p. 545). The main modifications result in long extrinsic retractor and long intrinsic levator and flexor muscles; these features are correlated with speedy movements in both Chilopoda and Lysiopetaloidea, although the details are different. These muscles give maximum displacements at the joints, and each muscle may telescope more than one joint, as in the Lysiopetaloidea.

The very long retractor prefemoris of *Polyxenus* (*ret.p.fe.* in text-fig. 4c and Part 5, text-fig. 2), from the postero-ventral edge of the prefemur to the Y-skeleton of the leg behind on the opposite side, parallels the somewhat similarly placed retractor trochanteris from the posterior margin of the trochanter to the sternite in Chilopoda (*ret.tr.s.* in Part 7), where the muscle slopes obliquely backwards, reaching the other side of the body in all but the Geophilomorpha.

The immobility of the coxa of *Polyxenus* was stressed in Part 5, pp. 166 and 181 in contrast to other Diplopoda, although the possibility of parasagittal rocking was suggested, p. 167. It is probable that the posterior margin of the bun-shaped coxa tips upward during the backstroke, thereby bringing the dorsal hinge line to an anterior position as in other Diplopoda and Chilopoda (p. 509). Such a movement is made possible by the deep folds of arthrodial membrane round the coxa and between the divided sternites, which may be regarded as specializations correlated with this basic need. An upward tilt during the backstroke could be caused by three muscles; the retractor prefemoris itself will tend to produce this tilt because its posterior insertion is more dorsal in position than the margin of the prefemur, muscle *e* (homologous with the normal diplopod retractor coxae, see Part 5, p. 166) pulls upwards on the posterior part of the coxa, and a rotator prefemoris from the posterior margin of the prefemur runs directly upwards to the ventral longitudinal muscle complex (*r.p.fe.* in text-fig. 4e) exactly like the rotator trochanteris of the Chilopoda, which passes upwards from the posterior margin of the trochanter to the pleural fold or to the tendon of the lateral longitudinal muscle (*r.tr.* in text-fig. 8 and Part 7). The levelling of the coxa during the forward stroke requires less force, and as in Chilopoda (text-fig. 8) can be effected by fewer muscles. Contraction of the original diplopodan protractor coxae (muscle *i*, text-fig. 4c and Part 5, text-figs 2, section *E* and 3A right side) must have this effect, possibly assisted by dorso-sternal muscle *d.s.b.* shown in Part 5, text-fig. 3. This remarkable functional similarity between muscles of different homologies, *ret.p.fe.*, *r.p.fe.*, *e.*, *i.* and *d.s.a.* in *Polyxenus* and *pct.1.*, *pct.2.*, *tep.*, *tcx.* and *plcx.* in a chilopod must indicate the occurrence of the all-important forward swing of the dorsal hinge line of the leg during the backstroke in *Polyxenus*, although the movement has not been demonstrated photographically as it has in the Chilopoda.

The intrinsic limb muscles are shown in anterior and posterior view in text-fig. 4c and e, where the muscles for clarity are drawn rather narrower than in life. Protractor prefemoris swings the leg forwards antagonizing the main stepping retractor prefemoris, as shown in Part 5. Depressor prefemoris and depressor femoris are large and long; the origin of depressor femoris from the Y-skeleton and not from the prefemur gives both length and stability since the trochanter and prefemur are so short and mobile. A retractor femoris, from the Y-skeleton to the posterior face of the femur, may be retractor in function but it could be a rotator supporting the action of rotator prefemoris. The typical diplopod pair of crossed muscles in the coxa and prefemur are not seen because a long levator postfemoris replaces the two normal levators and telescopes the dorsal coxa-trochanter, trochanter-prefemur and prefemur-femur joints, being attached to none of them, and gaining length by a dorsal insertion on the postfemur close to the dorsal hinge. These long levator and depressor muscles produce the large angular displacements of the proximal leg segments.

Three more distal muscles are present and all are long. The depressor post-femoris, arising from the Y-skeleton and traversing four leg segments, is reminiscent

of the long flexor muscles to the postfemur, tibia and tarsus in various Nematophora (text-figs 19-21). Flexores tibiae and tarsi appear to be united into one long muscle also traversing four segments. It arises on the posterior face of the femur and inserts ventrally on the tibia and on tarsus 1 and 2, thus appearing to be a modification of the usual long posterior components of diplopod flexors, although no other diplopod or chilopod has been found to possess a flexor muscle to tarsus 2. Long flexors characterize the Nematophora but the details differ from *Polyxenus*. The longest muscle system of *Polyxenus* is that of flexor unguiculi. The claw apodeme extends through four segments, its muscles fanning out over the dorsal face of the tibia and postfemur and the anterior face of the femur, the posterior face of this segment being occupied by retractor femoris and flexor tibiae-tarsi. In other Diplopoda flexor unguiculi fibres do not extend so far along the leg, but may traverse five leg segments in the Chilopoda (text-fig. 6) where the claw apodeme may end in the femur in *Lithobius* or on an apodeme from the anterior coxa-trochanter hinge in Geophilomorpha.

Thus the limb muscles as well as the joints of *Polyxenus* are basically diplopodan in nature, but are more specialized for giving speedy movements and wide angles of leg swing than those of any other diplopod, and show striking convergencies with the legs of the Chilopoda and Lysioptaloidea. The limbs of *Polyxenus* show no primitive diplopodan features or features which might be considered phylogenetically intermediate between those of Chilopoda and Diplopoda. *Polyxenus* is unique among Diplopoda in using the more or less vertical axis of leg articulation to give the long stride shown in text-fig. 3*d*, an articulation used by the fleet Lysioptaloidea and Chilopoda, and also the coxal rocking movement which represents the horizontal axis of limb articulation shown in text-fig. 3*a* and *c* which is a basic diplopodan movement. The Chilopoda employ both movements also, but by different means.

CONCLUSIONS, EVOLUTION OF THE LEG MORPHOLOGY IN DIPLOPODA AND EFFECTS OF SIZE ON LIMB STRUCTURE.

The survey of the leg skeleton has shown the same essential features throughout the Diplopoda in spite of numerous specializations meeting functional needs. The seven leg segments and their joints differ from those of the Chilopoda. The joints consist of : (1) The coxa-body union with two or with one point of tight articulation, the latter being the secondary condition (Oniscomorpha and Nematophora). This joint allows movement in only one of two planes. A simple type of coxa-body articulation, such as seen in the Colobognatha, could have given rise to the more specialized types. The robust articulations of Iuliformia and Polydesmoidea are suited to slow strong leg movements, and the almost vertical axis of articulation in Polydesmoidea makes long strides possible and considerable fleetness. The narrow coxal base in Iuliformia contributes towards the largest practicable angle of swing of the leg. (2) Three pivot joints or their derivatives, a reduction in number occurring on secondary fusion of the trochanter with the coxa. (3) At least four hinge joints, a fifth being formed in fleet forms by division of the tarsus (Lysioptaloidea and Pselaphognatha).

The basic type of leg skeleton serves the primitive diplopodan pushing habit, and the most marked divergencies from this type are found among the fleetest species. The nematophoran unilateral axis of coxal articulation suits rapid but weaker movements, and the narrow coxal base of the Lysioptaloidea represents the culmination of secondary acquisition of fleetness, and entails a loss of a conspicuous ability to push. The pselaphognathan changes are even more divergent (see p. 543). Longer legs, aiding fleetness but hindering burrowing, are obtained in much the same way in different orders, but increased mobility allowing wider displacements at the joints is obtained by different means in the several groups, and with the exception of the Polydesmoidea, at the expense of strength. Polydesmoidean joints with synovial cavities are remarkable achievements for an arthropod, and combine considerable mobility with great strength.

The survey of limb musculature of Diplopoda has shown the existence of a basic and widespread arrangement of muscles suiting the characteristic strong slow movements, and consisting of : (1) An antagonistic pair of extrinsic protractor and retractor muscles from the corresponding tracheal pouch. (2) Crossed direct levator and depressor muscles to the prefemur and to the femur. (3) Flexor muscles to the postfemur, tibia and tarsus, the anterior components being direct, and the longer posterior component of flexor tibiae and all of flexor tarsi crossing two joints. (4) Flexor unguiculi to the tarsal claw crossing two or three joints.

This pattern of musculature is modified in respect of a variety of needs :

(a) Increased size or increased strength of leg has led to existing muscles spreading out so that they contain more bundles (Iuliformia and Polydesmoidea) and additional muscles may appear (*Platyrhacus*).

(b) Increased size of leg or greater precision of movement is correlated with the presence of intrinsic retractors (p. 533), and additional extrinsic muscles in Colobognatha, necessitated also in Oniscomorpha by the presence of the flexible pedigerous lamina.

(c) Increased fleetness by a more loosely articulated leg possessing emarginated segments is associated with (i) an extrinsic longus retractor muscle to the coxa (Lysiopetaloidea) or prefemur (Pselaphognatha), (ii) extrinsic longus protractor muscle (Lysiopetaloidea), (iii) extrinsic rotator muscles, some new, some formed by the original protractor and retractor coxae of Pselaphognatha, (iv) intrinsic longus levator muscles, (v) intrinsic longus flexor (Lysiopetaloidea) and depressor (Pselaphognatha) muscles, (vi) protractor muscles (Lysiopetaloidea) which are not simply anterior extensions of the flexors as under (a) above, (vii) a retractor femoris which also stabilizes and braces the leg. All these features contribute to maximum strides and increased speed of movement. They are most marked in Lysiopetaloidea and Pselaphognatha, but some occur to a lesser degree in isolated examples from other orders. That such musculature is farthest removed from the basic type and not primitive is shown by the very different details in the several groups. The progressive formation of a longus flexor muscle in Nematophora, culminating in that of the Lysiopetaloidea, leaves the tibia with no ventrally inserted flexor, and the formation of longus muscles in *Polyxenus* leaves joints without local muscle insertions dorsally. Such an unusual state can hardly be regarded as primitive, and the curious disposition of muscles within the coxa in Nematophora, together with the progressive reduction of the extrinsic brevis muscles in this group, can only be regarded as specializations serving functional needs. A single extrinsic pair of wide brevis retractor and narrower brevis protractor muscles appears to be primitive in diplopods and serves strong slow movements. Longus muscles are added where wide displacements as well as strength are required (Polydesmoidea) and the smallest brevis muscles occur in Lysiopetaloidea and Pselaphognatha (muscles *i* and *e*), where wide displacements but not strength are evident, and these primitive muscles now play a subsidiary role. Long extrinsic muscles alone are present in Geophilomorpha, Scolopendromorpha and Lithobiomorpha, greater in number than in diplopods, while the Scutigermorpha have acquired additional short as well as long muscles and extra apodemes to control their very long legs, a condition appearing to be more specialized and furthest removed from a primitive state than that of any other chilopod (Part 7).

(d) The lateral position of the leg of Polydesmoidea has necessitated a long extrinsic levator muscle, as in Chilopoda (p. 530) and this is clearly a secondary condition for the diplopod.

A striking parallel exists between the structure and movements of the legs of *Pselaphognatha* and *Chilopoda*. In both (1) the telopodite is suspended from an anterior hinge built from a Y-shaped skeletal bar, (2) a rotator muscle pulls on the posterior side of the telopodite in a similar manner, (3) muscles rock or rotate the coxa and so bring the dorsal hinge line of the leg forward during the backstroke,

(4) the necessary cuticular flexibility exists, in the pleuron of Chilopoda and in the deeply folded soft pedigerous lamina of the Pselaphognatha, and (5) long extrinsic retractor and levator muscles and long intrinsic flexors move the legs in a comparable manner. These specializations result in a large angle of swing of the leg, only equalled among Diplopoda by the Lysiopetaloidae, and obtained by them in another manner ; but the differences in detail indicate that these structural and functional similarities are no more than convergencies.

Further support is thus given for the view expressed in Part 5 that the Pselaphognatha represent most specialized Diplopoda and are in no way intermediate between the Chilopoda and Diplopoda. The musculature of *Polyxenus* is in fact so specialized that it has needed a study of the limbs of all types of chilopods and diplopods before an assessment could be made of the significance of its details.

Segmentation of limbs and muscles. Verhoeff (1903, etc.) considered a diplopod leg with the fewer segments to be the more primitive, that long muscles are also primitive, and that short muscles have evolved under the influence of progressive subdivision of the skeleton which has induced division of the muscles.

Reasons have been given for supposing that the trochanter in Diplopoda and Chilopoda is a true segment, and that it has either become fused with the coxa or with the trochanter, or become specially mobile, according to functional needs (p. 506). The joint between tarsus 1 and tarsus 2 is clearly phylogenetically young, and only in the Pselaphognatha has tarsus 2 acquired a muscle of its own. The number of leg segments of Diplopoda must date from the time when the ventral origin and acute S-shaped flexure of the leg were adopted by ancestral burrowers ; such a leg needs a basic seven segments in contrast to the chilopodan six which are sufficient for the lesser flexures of a laterally projecting leg, six and five segments are present in the legs of Pauropoda and Symphyla respectively and in both the leg either projects freely or the animal stands well off the ground, S-shaped flexures being minimal.

That muscles are essentially plastic organs can be appreciated from the many different modifications already mentioned which are correlated with functional needs. The view that indirect long muscles are generally more primitive than direct short muscles, and the various proposed phylogenies of muscles in Chilopoda and Diplopoda based upon this assumption appear to be untenable. The diplopod flexor tibiae is direct anteriorly and indirect posteriorly, and this is connected with no skeletal subdivision. The widespread occurrence of the same plan of diplopod muscles, summarized above in features 1-4 which serves the basic pushing habit of the group may be taken as primitive for Diplopoda. It includes direct muscles except for part of flexor tibiae, flexor tarsi and flexor unguiculi. The latter is the longest muscle complex, and further increases in length occur in the apodeme rather than in the muscle of long-legged species (text-figs 17-21). The similar form of flexor unguiculi outside as well as within the Diplopoda indicates the long standing nature of this flexor. In contrast, the long muscles listed under *c* and *d* above differ in the various groups in which they occur, and their presence is always associated with a secondary need for increased displacements at the joints by fleeter forms ; thus these long muscles cannot be considered primitive. It may be suggested that the indirect telescoping of the joint between tarsus 1 and 2 by a remote muscle is a primitive state but that the indirect telescoping of joints, which may accompany the secondary formation of long muscles (pp. 533, 539, 543) are secondary. The significance of differences between the legs of Diplopoda and other Arthropoda will be considered after the completion of further functional studies.

Size. Many lines of work have shown how the size of an animal is related to the plan of its morphology and to the physical properties of its parts, and within each morphologically similar group of species there is a limited range of size over which the animals are efficient. That Diplopoda are efficient pushers only within certain size limits

was shown in Part 4, p. 343. Myriapodan skeleto-muscular systems differ from those of vertebrates in many ways besides size. The numerous legs of myriapods, which are operated by large numbers of minute muscles, contrast with the fewer larger locomotory muscles of vertebrates which are functionally the more appropriate for the larger type of animal.

The muscular dynamics of myriapods probably resemble those of larger animals in many ways, but the small inertia appertaining to their systems gives greater uniformity in the speeds of action of their parts than in vertebrates. The minimal pace durations of a *Blaniulus* 0.007 g. and a *Cylindroiulus* ten times this weight are about 0.6–0.7 sec., and those of a very large iuliform diplopod of 44 g. and 300 mm. length are about 0.8 sec. This uniformity over a size range of more than 6000-fold results in linear relationships between animal lengths and speeds over considerable size ranges, and contrasts with the vertebrates where the inertia of muscles and bones causes animals of similar morphology to run or swim at about the same rates irrespective of size because the frequency of the locomotory movements are inversely proportional to body length. J. V. Cousteau's film "The Silent World" shows the tail beats of porpoises and sperm whales to be about 0.5 and 4–5 sec. duration respectively, a whale of about 150 tons being about 1000 times heavier than a porpoise of 300 lbs. In contrast to mammals the diplopod inertia of skeleton and muscles appears to be of little significance for locomotory movements. Greater velocities of movements are found in insect wings and halteres, and although the sizes of the parts may be smaller, inertia here is no longer a negligible factor.

It is advantageous for a fleet mammal to possess short muscles. The pocket gopher, kangaroo rat and jerboa with increasing length of leg show an increase in the linear dimensions of tendon and bone but not of muscles (Howell, 1932). The horse and *Dasypros* when scaled to the same size show *m. teres major* to be about the same length in the two, although it serves quick weak movements in the horse and strong slow ones in *Dasypros* (Maynard Smith & Savage, 1956). But the presence of the longer muscles in myriapods is correlated with the speedier movements giving fleetness because the inertia appertaining to their skeleto-muscular systems is so small. The larger mammals become, the greater is the abundance of their elastic tissue, so conspicuous in the horse and elephant. It is possible that important elastic properties lie in the trochanter of fleet myriapods (p. 522 and 535), although there is no conspicuous provision for elastic storage of energy in other myriapods. Size alone may account for these differences.

The usual absence of intrinsic extensor muscles to the distal three or four leg segments in myriapods is also dependent upon size. Only one instance has been found (*Platyrhacus*) of extensor muscles in this position, and these have a special function, (p. 542). This economy in extensors enables a maximum amount of muscle to serve propulsive retraction, an economy made possible by a variety of details of the skeleto-muscular systems.

Design of body and function. The mechanical efficiency, i.e. $\frac{\text{work done}}{\text{total energy used}}$ is maximal at about 0.2 of the maximum speed against a load of nearly half the maximum in vertebrates; each muscle is designed for maximum power and efficiency within its most usual range of speed, and if that speed is exceeded power and efficiency fall off (Hill, 1950). Similar features doubtless characterize myriapodan systems. The reluctance of chilopods to run their fastest and diplopods to exert their slowest strongest movements are probably correlated with a falling off of efficiency outside the commonest range (see also Part 3, p. 130). The more usual movements, which are neither very fast nor very strong, are probably those which are performed with the greatest mechanical efficiency, but it is the ability to perform actions at great cost which has directed skeleto-muscular evolution. Howell's (1944) statement that "it is probably not the easy movements of everyday life that are chiefly instrumental in

shaping the muscular and osseous pattern but the critical potential that is usually held in reserve" is a conclusion directly parallel to the suggestions made in Part 5, p. 183 and equally applicable to the Myriapoda.

The diplopodan correlations between leg design and function are just as striking and all embracing as those appertaining to the trunk (Parts 4 and 5) although on first inspection may be less easy to apprehend. The data showing how it has been possible for a diplopod to evolve legs capable of performing functions opposite from those of its ancestors, together with the other conclusions, will be of service in understanding leg structure and phylogeny of Arthropoda, with particular reference to Chilopoda, Symphyla and the several hexapodous groups.

MECHANICAL PROPERTIES OF CUTICLE.

Richards (1951) has noted that elastic properties of chitin are "of inestimable biological importance, and yet almost no quantitative data are available": similarly in respect of the property of hardness "the terms hard and soft are only relative and without quantitative meaning". No precise data can be offered to fill this gap in our information, but it may be useful to record some mechanical properties and the distribution of the various cuticular states which have been encountered in the present work. Mechanical properties associated with the various degrees of sclerotization and impregnation may be expected to grade into one another, just as do the staining reactions. Mechanical properties in a biological sense will also depend on the thickness of the type of cuticle even if its composition is the same.

Calcification in diplopods may be so heavy as to render the body sclerites and leg segments practically inflexible, and they crack sooner than bend when a deforming force is applied. Decalcified diplopod sclerites bend more easily than the tergites of *Lithobius* which are more fully sclerotized (see text-fig. 2A Blower, 1951); these properties are correlated with needs (p. 492, and Parts 3 and 4). If a chitinous layer can bend at all there must be either expansion on the convex side or compression on the concave side, or both, even if the layer as a whole is apparently unstretchable. A chitinous lamina which is non-stretchable exhibits elasticity, and returns to its original curvature when deforming forces are removed. A chitinous layer which can be easily compressed or stretched as a whole does not exhibit much elasticity.

The *non-staining refractile* zone of fully sclerotized cuticle covering the sclerites of Diplopoda and Chilopoda is usually continuous over the arthrodial membranes of the whole body although it is less evident on the pedigerous lamina of *Polyxenus* (Part 5, text-fig. 7g). Blower (1951) records the absence of this zone over the intucked pleural membranes of *Haplophilus*. When thin this refractile cuticle is clearly flexible, since it covers the thick unmodified cuticle of arthrodial membranes (text-figs 9, 11, 13 and 14) and alone forms the cuticular link between the tergites of *Polyxenus* (Part 5, text-fig. 8o). When thick this refractile cuticle does not readily bend; it forms the tarsal claw of most diplopods and the distal parts of many spines (*Polydesmus*, text-fig. 15k) where bending may be unsuitable.

Refractile cuticle appears to be comparatively unstretchable. Eastham (1955) has shown how the two longitudinal membranes spanning the cavity of the galea of *Pieris* do not change in length or breadth when the galea rolls up and unrolls, and their non-staining reactions with Mallory and refractile appearance suggest a basic similarity with the cuticular layer. In the Crustacea *Hemimysis* and *Nebalia* very thin refractile struts link the foregut to the skeleton and they may be similarly non-stretching. It is probable that the thin refractile surface layer of cuticle in diplopods may be also non-stretchable, and that this property may be of importance in preventing non-elastic very flexible cuticle of leg joints (pale blue-staining with Mallory) from being pulled out of shape.

Bending of thick arthrodial membranes probably takes place by a compression or expansion of the inner parts of the unmodified cuticle, the surface refractile zone

maintaining the same linear dimensions. The movements of the arthrodial membranes between the leg segments is such that the surface of the membrane is mostly flat or convex. Concave bending occurs more readily on the inter-diplosegment arthrodial membrane, and in the folds of the pleuron and on both sides of the coxa of Chilopoda, and here the surface of the refractile layer is usually complex and possibly facilitates these flexures (text-fig. 11*b* and Blower, 1951, text-fig. 2*C*). No such surface elaborations occur on the underside of the posterior edge of the chilopod tergite (the intermediate sclerites in text-figs 1*A* and *B*, 2*B* and 3, Blower, 1951) where concave bending does not occur. The ventral side of the outstretched galea of *Pieris* shows a marked folding of the refractile cuticle forming numerous transverse furrows while corresponding dorsal furrows are slight. On rolling up linear changes of the galea are greater ventrally, the folds of the outer cuticle becoming deeper. The furrows which are clear in the straight proboscis probably facilitate this rolling up by easing ventral compression and limiting the movement to one plane. The many surface humps of refractile cuticle over arthrodial membranes of chilopods, most conspicuous on the pleuron and smallest at limb joints, may facilitate bending in any direction by providing incipient lines of folding. Similar flexibility is given by the surface humps in *Peripatus* over each ectodermal cell which are formed in another manner.

The presence practically everywhere of the refractile layer in the surface of the body cuticle is correlated also with the fact that a fully sclerotized zone alone is capable of carrying the lipid material which renders the surface hydrofuge. This lipid layer is thickest in those Myriapoda which have the most hydrofuge cuticles, the burrowing Iuliformia and Geophilomorpha, in contrast to the more surface-living Polydesmoidea and Lithobiomorpha (Blower, 1955).

Thus it may be suggested that refractile cuticle is the most elastic and least stretchable cuticular state; that it is needed over almost all external faces by virtue of its carrying the hydrofuge agent; and that in order to be flexible the layer must be very thin, or be broken up into inwardly projecting cones as in Geophilomorpha.

Cuticle staining red with Mallory is less fully sclerotized, it may appear amber in life and is situated usually underneath the surface refractile layer, and varies greatly in thickness and distribution. It is usually present in body scutes, and in greater thickness where calcification is not the principal stiffening agent; the limb segments of Chilopoda predominantly stain red while those of Diplopoda stain blue with Mallory (text-figs 11*b* and 14*a* and *b*), although some red can be seen in the legs of the larger Diplopoda. Entire spines or only their bases may be composed of red-staining cuticle (text-figs 9 and 15), and increased sclerotization exists near hinges and distal extremities of limb segments in both Chilopoda and Diplopoda (p. 524).

It is probable that red-staining cuticle is particularly elastic, but less rigid and more stretchable than non-staining cuticle. Its elastic properties account for the rolling up of the proboscis of a butterfly (Eastham, 1955) and for adhesion to the substratum by the thin adhesive lappet of the claw of *Polyxenus* (Part 5, see also p. 529). Where a small length of arthrodial membrane is present at a tight hinge joint, elasticity on both sides of this region must facilitate smooth working (text-figs 14 and 15). In the incomplete joint across the tarsus of Lysipetaloidea elasticity of the dorsal patch of red-staining cuticle allows a ventral intake at the joint under pressure from flexor unguiculi, and a return to the extended state when the deforming force is removed. The probable elastic significance of the marginal zones of red staining cuticle at the distal ends of leg segments (text-figs 14 and 15) has been referred to on p. 524, and the distal part of the trochanter in Chilopoda (text-fig. 11*b*) where two layers of red staining cuticle are separated by unmodified cuticle, again suggests an elastic function for the red-staining cuticle (p. 522).

The great flexibility and strength of the anterior hinge between coxa and trochanter in Chilopoda resides in the properties of the amber portions of the Y-skeleton and trochanter bars which are invested by transparent thin portions of fully sclerotized

cuticle. The detailed morphology of these joints is very difficult to apprehend. The corresponding Y-skeleton of the *Pselaphognatha* stains blue with Mallory ; presumably these much smaller animals need a greater degree of flexure per unit length of cuticle, this is obtained by a lesser degree of sclerotization which also gives sufficient support.

Cuticle staining pale blue with Mallory forms the greater part of arthrodial membranes. Manipulation of this cuticle when devoid of muscles shows that it is very flexible and non-elastic. It may be much thicker than the scutes (text-fig. 9d) owing to the changes caused by tanning which renders sclerotized cuticle thinner.

Unmodified cuticle serves freedom of movement, and occasionally it carries important muscles, although the bulk of the musculature is inserted upon the scutes. The retractor paratergalis of *Polycenus* is attached to unmodified cuticle (Part, 5 p. 161 and text-figs 2 and 8q). The "pleural fold" of Chilopoda (Part 7) provides an essential zone of support to which is attached a number of muscles, either directly (Geophilomorpha) or indirectly (Lithobiomorpha) where the tendon of the lateral longitudinal muscles sinks away from the surface and is united to the pleural fold by a number of short muscles (*i.m.*, Part 7). In the Geophilomorpha tendinous extensions of the dorsal intersegmental arthrodial membranes provide insertions for the dorsal longitudinal muscles which are too bulky to find place on the tergites themselves.

Cuticle staining dark blue with Mallory shows intermediate mechanical properties between those of arthrodial membranes and more fully sclerotized cuticle staining red. Endoskeletal bars and struts usually stain dark blue, and the bulk of the cuticle of leg segments and body in the smaller Diplopoda is of this type. The blue staining reaction becomes more intense where blue grades into red at the distal ends of leg segments. Calcification of this dark blue cuticle in diplopods gives rigidity, while similar locations are stiffened by further sclerotization in Chilopoda.

Cuticular specializations combining mobility with greater rigidity and strength than is possessed by an arthrodial membrane are developed by similar devices in widely separate groups, and indicate the mechanical properties of the parts. The burrowing ability of Geophilomorpha depends on great shape changes of each segment, a thrust on the ground being transmitted from the body surface which must therefore be strong. When the body shortens a longitudinal convexity develops on the short tergites, and paratergites and pleurites change their apparent size and shape by alterations in the extent of the intucked edges of the scutes; a mobile but very complete armour of pleurites exists in larger species such as *Orya barbarica* (Part 3, Pl. 31, figs 15 and 16 and Part 7). Duboscq (1898) and Fahlander (1938) have given figures of the cones of exocuticle which project into the unmodified cuticle below, and Blower (1951) has described the condition more fully. The cones gradually become smaller and disappear in the transitional zones towards arthrodial membranes, and tend to merge with the general increase of sclerotization in the middle parts of the scutes where shape changes are least. Such an arrangement gains rigidity from the presence of the cones and mobility in any direction by bending of the unmodified cuticle between the cones.

A fundamentally similar device is found in the galea wall of the food tube of *Pieris*, but flexibility here is limited to one plane. Instead of cones there are bars of exocuticle projecting into the flexible unmodified cuticle (Eastham, 1955), these bars are thinner on the ventral than on the dorsal side of the food tube, and clearly the greater linear change occurs ventrally where the exocuticle is folded. The cones in Geophilomorpha and the bars in *Pieris* both stain red-orange with Mallory and must be stiff and elastic, a cuticle with a continuous layer of red-staining material of this thickness would be incapable of acute bending.

SUMMARY.

1. The habits of life, use of coxal sacs, locomotory performance and pushing ability of several species of *Lysiopetaloidea* are recorded for comparison with other *Diplopoda* (Parts 4 and 5).

2. The *Lysiopetaloidea* represent, not a primitive group of diplopods, but a highly specialized one in which leg morphology has radically changed in association with altered habits of life.

3. The fleetier *Diplopoda* and *Chilopoda* use long strides and large angles of swing of the legs compared with diplopods performing strong slow movements, skeletal-muscular specializations permitting the wide swing.

4. A horizontal axis of swing between coxa and body gives a short stride suiting slow strong movements (most *Diplopoda*) and a vertical axis of swing of the coxa may give double the stride length for the same angular displacement, so suiting fast movements which are also weak in *Chilopoda* and *Nematophora* and fairly fast but strong in *Polydesmoidea*.

5. Both horizontal and vertical axes of coxal swing are combined in the leg movements of *Chilopoda* and *Pselaphognatha*, resulting in large angles of swing of the leg.

6. The horizontal coxal axis gives greatest strides when the body is far from the ground and strongest movements when the body is close to the ground (*Iuliformia* etc.). The vertical coxal axis gives greatest strides when the body is close to the ground (*Chilopoda*, *Polydesmoidea*, *Nematophora* and *Pselaphognatha*).

7. An ability to flex the leg acutely in an S-shape is needed by most *Diplopoda* and entails morphological specializations. The proximal part of this bend is unnecessary to *Chilopoda* and less needful to *Polydesmoidea* and *Pselaphognatha*.

8. The stance, the shapes and lengths of leg segments, and the types of joints and their distribution are shown to have functional significance. Loose articulations at the joints permit maximal flexures and facilitate speedy movement of the parts, while tight articulations restrict the flexures but increase the strength of the leg.

9. A basic similarity exists between the superficially dissimilar chilopod and diplopod pivot joints from the coxa to the prefemur or coxa to trochanter. The highly specialized anterior components of a pivot joint form the costa coxalis and the very flexible but weak hinge between trochanter and coxa of *Chilopoda*, which allows rapid wide movements.

10. Hinge joints from prefemur to claw are strengthened in similar ways in the fleetier *Diplopoda* and *Chilopoda*, and synovial cavities within all types of joints of *Polydesmoidea* combine mobility with strength in this group alone.

11. The functional significance of the so-called incomplete coxal cylinder in *Chilopoda* is described. The suggestion is made that the pleurocoxa of *Chilopoda* represents an integral specialized part of the coxa and not a pleural scute.

12. The probable evolution of the trochanter segment is discussed. It appears to be a true segment which has become partially fused either to coxa or trochanter, or has become especially mobile, according to functional needs, in *Diplopoda* and *Chilopoda*.

13. A divided tarsal segment providing an extra joint serves fleetness, and has been independently acquired in the faster *Diplopoda* and *Chilopoda*.

14. Anterior pivot joint components and dorsal hinge joints form two incompressible axes of the leg which transmit the thrust to the ground throughout the backstroke.

15. A forward rotation of the dorsal hinge-line of the leg during the latter part of the backstroke is an essential movement. It results from the nature of the coxal swing about an approximately horizontal axis in *Iuliformia*, *Colobognatha* and *Onisco-morpha*, it is obtained by a slight fixed tilt of the approximately vertical axis of coxal

swing in Nematophora, and by muscles causing an active rotation of the leg in Pselaphognatha and Chilopoda. This extensive movement in Chilopoda is a factor accounting for their superiority in speed over all Diplopoda.

16. The small size of skeleto-muscular units of diplopod and chilopod limbs gives rise to certain differences from the systems of larger vertebrate animals. An important physical difference appears to concern the lesser inertia of myriapodan systems, which leads in many cases to almost linear relationships between speed and size over considerable ranges of size in contrast to vertebrates.

17. Intrinsic and extrinsic muscles are short and wide in legs exerting slow strong movements, and are longer and narrower in legs providing rapid weak movements, in contrast to vertebrates. The weakness of muscles giving rapid movements is compensated for by an increase in the number of extrinsic muscles in the fleeter Diplopoda and Chilopoda.

18. The basic plan of the musculature of diplopod limbs serves slow and strong movements (summarized on p. 545).

19. A comparative and functional account is given of the limb musculature throughout the Diplopoda. Secondary modifications resulting in speedy movements are most extreme in the Pselaphognatha and Nematophora culminating in those of the Lysiopetaloidea where they have evolved at the expense of a marked ability to push (summarized on p. 545).

20. The skeleto-muscular systems of the fleeter Diplopoda differ in detail in each group, long extrinsic retractors and long levators and flexors being achieved in different ways (summarized on p. 545).

21. The many similarities between limb skeleton and muscles of the Pselaphognatha and Chilopoda are superficial, the details differ and have been convergently acquired in meeting similar needs. The pselaphognathan limb is basically diplopodan in structure, although more specialized than in any other order.

22. The larger number of leg segments in Diplopoda than in other Myriapoda was probably established early when the ancestral stock acquired both the mid-ventral origin and the acute S-shaped bend of the leg. No support is found for the suggestion that a smaller number of leg segments is primitive in this group, or that long indirect muscles are usually primitive.

23. The mechanical properties of the different states of cuticle encountered in the present work are recorded.

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KEY TO LETTERING.

<i>a.k.co.</i>	knob on anterior side of coxa forming a component of coxa-trochanter pivot joint (<i>P.1.</i>).	<i>d.s.c.</i>	dorso-sternal muscle to outer edge of coxa.
<i>a.k.p.fe.</i>	knob on anterior side of prefemur forming a component of prefemur-femur pivot joint (<i>P.3.</i>).	<i>d.gl.</i>	ducts of epidermal glands.
<i>a.k.tr.</i>	knob on anterior side of trochanter forming a component of trochanter-prefemur pivot joint (<i>P.2.</i>).	<i>dep.fe.</i>	depressor femoris.
<i>a.p.</i>	flexible anterior process from claw.	<i>dep.fe.a.</i>	anterior part of depressor femoris.
<i>a.r.fe.</i>	articulating process on anterior side of femur forming a component of prefemur-femur pivot joint (<i>P.3.</i>).	<i>dep.fe.p.</i>	posterior part of depressor femoris.
<i>a.r.p.fe.</i>	articulating process on anterior side of prefemur forming a component of trochanter-prefemur pivot joint (<i>P.2.</i>).	<i>dep.p.fe.</i>	depressor prefemoris.
<i>a.t.p.</i>	anterior tracheal pouch.	<i>dep.p.fe.a.</i>	anterior strand of depressor prefemoris.
<i>am.</i>	arthrodial membrane.	<i>dep.po.fe.</i>	depressor postfemoris.
<i>ax.</i>	axis of swing of coxa on sternite.	<i>dep.tr.</i>	depressor trochanteris.
<i>b.p.</i>	breaking plane.	<i>dep.tr.g.</i>	depressor trochanteris of Geophilomorpha from sternite.
<i>c.c.</i>	costa coxalis.	<i>ect.</i>	ectoderm.
<i>co.</i>	coxa.	<i>f.</i>	tendinous fibrils between muscle and cuticle.
<i>co.a.</i>	fold on coxa which is gripped by sternal lobe <i>s.l.</i>	<i>fe.</i>	femur.
<i>co.an.</i>	anterior curved face of coxa.	<i>fl.po.fe.</i>	flexor postfemoris.
<i>co.e.a.</i>	anterior edge of coxa.	<i>fl.po.fe.a.</i>	anterior part of flexor postfemoris.
<i>co.e.p.</i>	posterior edge of coxa.	<i>fl.po.fe.p.</i>	posterior part of flexor postfemoris.
<i>co.f.</i>	flattened posterior facet on coxa.	<i>fl.ta.</i>	flexor tarsi.
<i>co.h.</i>	coxal thickening forming part of tight coxa-sternite articulation.	<i>fl.ta.fe.</i>	flexor tarsi to femur.
<i>co.ip.</i>	eucoxa inferior and posterior.	<i>fl.ta.fe.a.</i>	anterior part of flexor tarsi to femur.
<i>co.m.</i>	flat mesial facet of coxa.	<i>fl.ta.fe.p.</i>	posterior part of flexor tarsi to femur.
<i>co.n.</i>	notch on coxa which is gripped by lobe of sternite (<i>s.m.l.</i> in text-fig. 7f).	<i>fl.ta.l.</i>	flexor tarsi longus.
<i>co.p.</i>	posterior curved face of coxa.	<i>fl.ta.po.fe.</i>	flexor tarsi to postfemur.
<i>co.ri.</i>	posterior ridge on coxa.	<i>fl.ti.</i>	flexor tibiae.
<i>co.s.</i>	proximal thickened rim on coxa.	<i>fl.ti.a.</i>	anterior part of flexor tibiae.
<i>co.s.r.</i>	curved ridges on coxa gripped by sternite lobe.	<i>fl.ti.l.</i>	flexor tibiae longus.
<i>co.s.1-co.s.4</i>	range of parasagittal movement of eucoxa superior.	<i>fl.ti.p.</i>	posterior part of flexor tibiae.
<i>co.sa.</i>	coxal sac.	<i>fl.ti.po.fe.l.</i>	flexor longus to tibia and postfemur.
<i>co.sh.</i>	tight part of articulation between coxa and sternite.	<i>fl.ti.ta.</i>	flexor to tibia and tarsus.
<i>co.su.</i>	eucoxa superior.	<i>fl.un.</i>	flexor unguiculi.
<i>co.x.</i>	anterior angle on proximal rim of coxa.	<i>fl.un.a.</i>	anterior part of flexor unguiculi.
<i>d.p.l.</i>	dilatation of pedigerous lamina.	<i>fl.un.p.</i>	posterior part of flexor unguiculi.
<i>d.s.a.</i>	dorso-sternal muscle to transverse tendon.	<i>fl.un.po.fe.</i>	flexor unguiculi to postfemur.
<i>d.s.b.</i>	dorso-sternal muscle to outer ramus of Y-skeleton.	<i>fl.un.t.</i>	tendinous apodeme of flexor unguiculi.
		<i>fl.un.ti.</i>	flexor unguiculi to tibia.
		<i>H.H.1.-H.5.</i>	dorsal hinges between leg segments.
		<i>i.a.m.</i>	inner lamella of arthrodial membrane.
		<i>i.r.t.p.</i>	inner ramus of tracheal pouch.
		<i>j.tr.p.fe.</i>	junction of trochanter and prefemur.
		<i>k.</i>	knob on sternite strengthening the tight part of coxa-ring articulation.
		<i>k.l.</i>	knob-like apodeme of levator muscle.
		<i>k.pl.r.</i>	range of parasagittal movement of katopleure.
		<i>l.a.</i>	anterior leg of diplosegment.
		<i>l.p.</i>	posterior leg of diplosegment.

<i>l.p.n., l.p.n.</i>	+ 1. posterior legs of diplosegments <i>n</i> and <i>n</i> + 1 respectively.	<i>plcx.</i>	remotor muscle from coxa to tendon of lateral longitudinal muscles.
<i>l.s.n., l.s.n.</i>	+ 1. legs of sternites <i>n</i> and <i>n</i> + 1 respectively.	<i>pln.</i>	arthrodial membrane of pleuron.
<i>lev.fe.</i>	levator femoris.	<i>po.fe.</i>	postfemur.
<i>lev.fe.d.</i>	levator femoris arising from dorsal proximal part of prefemur.	<i>pr.co.</i>	protractor coxae.
		<i>pr.co.(i).</i>	protractor coxae of <i>Polyxenus</i> (muscle <i>i</i> in Part 5).
<i>lev.fe.l.</i>	levator femoris longus.	<i>pr.co.b.</i>	protractor brevis coxae.
<i>lev.fe.l.a.</i>	proximal anterior strands of levator femoris longus.	<i>pr.co.l.</i>	protractor longus coxae.
<i>lev.fe.l.d.</i>	distal dorsal strands of levator femoris longus from dorsal face of femur.	<i>pr.fe.</i>	protractor femoris.
		<i>pr.p.fe.</i>	protractor prefemoris.
<i>lev.p.fe.</i>	levator prefemoris.	<i>pr.po.fe.</i>	protractor postfemoris.
<i>lev.p.fe.int.</i>	levator prefemoris internus.	<i>pr.ti.</i>	protractor tibiae.
<i>lev.p.fe.l.</i>	levator prefemoris longus.	<i>r.a.</i>	articular facet on ring.
<i>lev.po.fe.</i>	levator postfemoris.	<i>r.p.fe.</i>	rotator prefemoris.
<i>lev.ti.</i>	levator tibiae.	<i>r.pl.co.</i>	rotator pleurocoxae.
<i>lev.tr.</i>	levator trochanteris.	<i>r.tr.</i>	rotator trochanteris.
<i>o.a.m.</i>	outer lamella or arthrodial membrane.	<i>ret.co.</i>	retractor coxae.
		<i>ret.co.b.</i>	retractor coxae brevis.
<i>o.i.a.m.</i>	origin of inner lamella of arthrodial membrane.	<i>ret.co.(e).</i>	retractor coxae of <i>Polyxenus</i> (muscle <i>e</i> in Part 5).
<i>o.o.a.m.</i>	origin of outer lamella of arthrodial membrane.	<i>ret.co.l.</i>	retractor coxae longus.
<i>p.art.</i>	pair of articular facets allowing horizontal sliding coxa against sternite.	<i>ret.co.s.</i>	retractor of coxal sac.
<i>p.co.</i>	procoxa.	<i>ret.fe.</i>	retractor femoris.
<i>p.ect.</i>	pigment in ectoderm showing the extent of the epithelium.	<i>ret.p.fe.</i>	retractor prefemoris.
<i>p.fe.</i>	prefemur.	<i>s.</i>	sternite.
<i>p.fe.e.a.</i>	anterior edge of prefemur.	<i>s.a.n.1.</i>	anterior sternite of diplosegment <i>n</i> + 1.
<i>p.fe.e.p.</i>	posterior edge of prefemur.	<i>s.co.tr.</i>	synovial cavity in arthrodial membrane between coxa and trochanter.
<i>p.k.</i>	dorsal process which if enlarged might form an apodeme such as <i>k.l.</i> in text fig. 15 <i>l</i> .	<i>s.e.</i>	posterior edge of sternite.
		<i>s.fe.po.fe.</i>	synovial cavity in arthrodial membrane at femur-postfemur joint.
<i>p.k.tr.</i>	knob on posterior side of trochanter forming a component of trochanter-prefemur joint (<i>P.2.</i>).	<i>s.h.</i>	sternal part of tight coxa-sternite articulation.
<i>p.r.p.fe.</i>	posterior proximal ridge on prefemur forming component on pivot joint between trochanter and prefemur (<i>P.2.</i>) or its equivalent.	<i>s.l.</i>	edge of posterior median lobe of sternite.
<i>p.t.p.</i>	posterior tracheal pouch.	<i>s.l.a.n.1.</i>	socket of coxa of anterior leg of diplosegment <i>n</i> + 1.
<i>P.1.-P.3.</i>	positions of pivot joints.	<i>s.m.</i>	median boss on sternite.
<i>P.1.a., P.2.a.</i>	anterior components of pivot joints between coxa and trochanter and between trochanter and prefemur respectively.	<i>s.m.l.</i>	lobe from boss on sternite fitting between a pair of coxae.
<i>P.1.p., P.2.p.</i>	posterior components of pivot joints between coxa and trochanter and between trochanter and prefemur respectively.	<i>s.n., s.n.1., s.n.2.</i>	three successive sternites.
<i>pct.1.</i>	promotor muscle from eucoxa superior to tergite.	<i>s.p.n.1.</i>	posterior sternite of diplosegment <i>n</i> + 1.
<i>pct.2.</i>	promotor muscle from procoxa to tergite.	<i>s.po.fe.ti.</i>	synovial cavity in arthrodial membrane between postfemur and tibia.
<i>pl.</i>	prophragma.	<i>s.r.co.</i>	synovial cavity in arthrodial membrane between coxa and body.
<i>pl.co.</i>	pleurocoxa.	<i>s.tr.p.fe.</i>	synovial cavity in arthrodial membrane between trochanter and prefemur.
<i>pl.co.k.</i>	sclerotized knob on pleurocoxa.	<i>sc.</i>	patch of brown sclerotized cuticle forming hinge region of partial joint across tarsus.
		<i>st.int.</i>	sternalis intersecautus muscle.
		<i>t.</i>	tubercle above coxa strengthening tight part of coxa-ring articulation.
		<i>t.n., t.n.1.</i>	tergite of diplosegment <i>n</i> and <i>n</i> + 1 respectively.
		<i>t.p.</i>	tracheal pouch.

<i>t.s.H.</i>	transverse section through leg at a hinge joint.	<i>tr.e.a.</i>	anterior edge of trochanter.
<i>ta.</i>	tarsus.	<i>tr.e.p.</i>	posterior edge of trochanter.
<i>ta.1.</i>	tarsus 1.	<i>tr.k.</i>	sclerotized knob on proximal rim of trochanter representing posterior pivot joint component.
<i>ta.2.</i>	tarsus 2.		tight ventral part of coxa.
<i>tcr.</i>	remotor muscle from eucoxa superior to tergite.	<i>v.</i>	sternite articulation.
<i>te.</i>	tergite.	<i>v.s.</i>	ventral spine on coxa.
<i>tep.</i>	promoter muscle from katopleure to tergite.	<i>vlm.</i>	ventral longitudinal muscles.
<i>ti.</i>	tibia.	<i>w.</i>	articulating ridge of femur.
<i>tr.</i>	trochanter.	<i>y.</i>	Y-shaped sclerotized bar in coxa.
<i>tr.b.</i>	sclerotized bar forming trochanter component of anterior hinge (pivot joint) between coxa and trochanter.	<i>z.</i>	groove on postfemur near hinge.
		1-6	levels at which lines can be focused in whole mounts.

DESCRIPTION OF PLATE 9.

The black and the white spots mark legs in contact with the ground, and black lines show groups of legs performing the forward swing; "p.d." denotes phase differences between legs, that proportion of a pace by which leg "n" is in advance of leg "n + 1."

FIG. 22. *Blaniulus guttulatus* running quickly over glass, ventral view showing maximum angles of swing of the legs, gait (5·5 : 4·5). $\times 7\cdot25$.

FIG. 23. *Polymicrodon polydesmoides*, male, 17 mm., side view. $\times 5\cdot3$.

FIG. 24. *Dischopetalum illyricum*, 31 mm. long, running fast, in dorsal view, gait (6·9 : 3·1), p.d. 0·062, 9 legs off and 5 legs on the ground in each metachronal wave. $\times 3$.

FIG. 25. *Callipus longobardius*, female, 42 mm. long, dorsal view of anterior end, walking slowly, gait about (5·0 : 5·0), p.d. 0·1-0·7, 5 legs off, 5 legs on, 7 legs off and 7 legs on the ground in the posterior two metachronal waves shown. $\times 3$.

FIG. 26. *D. illyricum*, female, in the spiral position. $\times 3$.

FIG. 27. *Tachypodoiulus niger* running fast on glass, ventral view, gait (6·2 : 3·8), p.d. 0·077, 5 legs on, 8 legs off the ground in each metachronal wave. $\times 3\cdot3$.

FIG. 28. *Dischopetalum illyricum*, female, running slowly on glass, ventral view, gait (5·3 : 4·7), p.d. 0·058, 8 legs on and 9-10 legs off the ground in each metachronal wave. $\times 4\cdot9$.

FIG. 29. *Callipus longobardius*, female, running fast on glass, ventral view, gait (7·0 : 3·0), p.d. 0·070, 4-5 legs on and 9-10 legs off the ground in each metachronal wave, boot on one left foot. $\times 4\cdot9$.

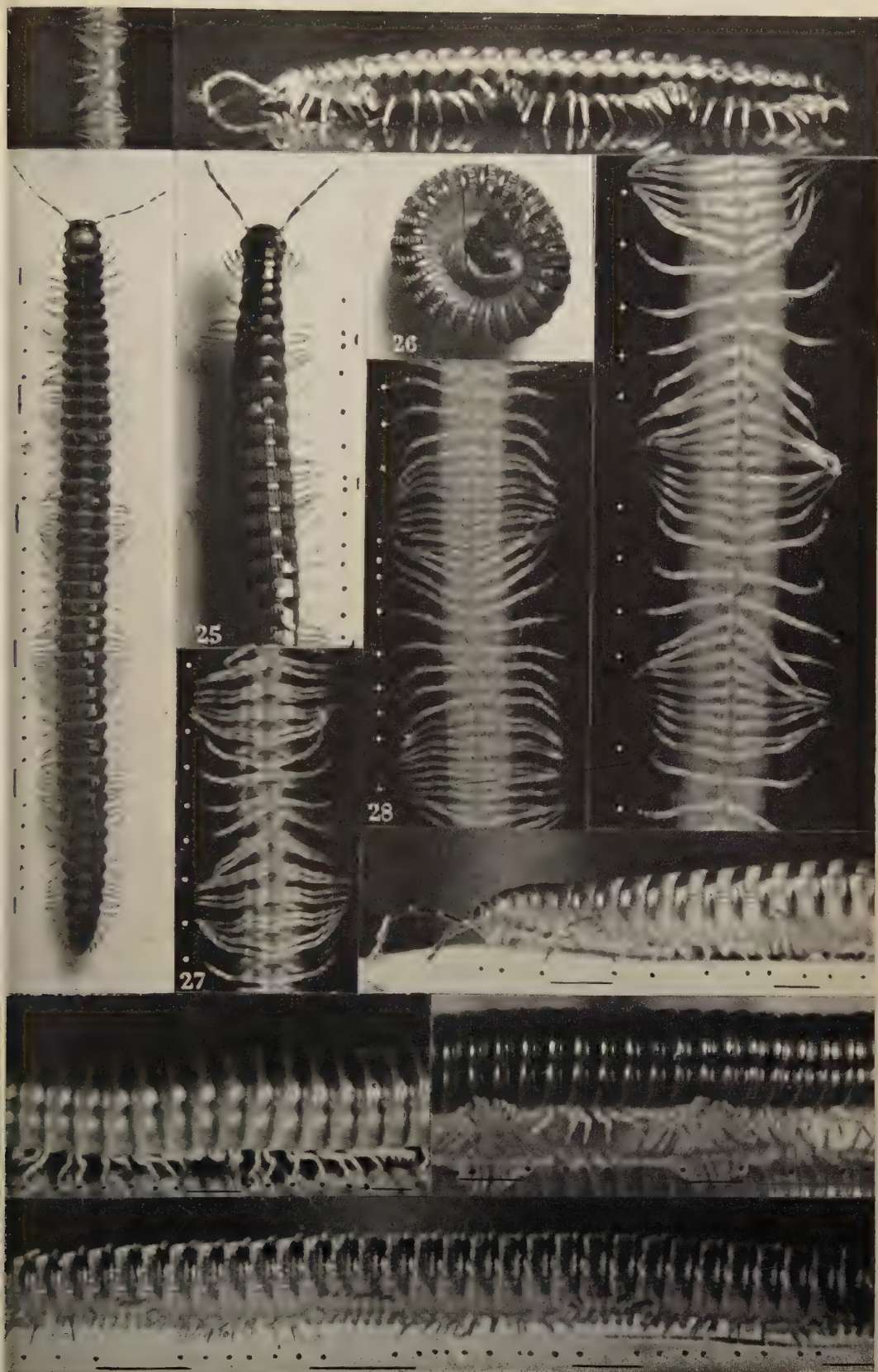
FIG. 30. *Callipus longobardius*, female, side view of head end, walking.

FIGS 31-33. Side view of walking millipedes, head ends to the left.

FIG. 31. *Cylindroiulus londinensis*, gait approx. (5·3 : 4·7), p.d. 0·07, 7 legs on, 8 legs off, 7 legs on and 7 legs off the ground in the two metachronal waves shown. $\times 4\cdot7$.

FIG. 32. *Plusioporus sulcatus*, gait approx. (6·3 : 3·7), p.d. 0·06, 11 legs off, 6 legs on, 11 legs off and 6 or 7 legs on in the two metachronal waves shown. $\times 1\cdot25$.

FIG. 33. *Dischopetalum illyricum*, female, gait approx. (5·3 : 4·7), p.d. 0·057, 8 legs off, 7 legs on, 11 legs off, 9 legs on, 8 legs off, 8 legs on the ground in the three metachronal waves shown; some legs of the other side of the body appear in shadow and are thus darker than the near side legs. $\times 3\cdot75$.



THE DEVELOPMENT OF THE CHONDROCRANIUM IN THE SEA-HORSE, HIPPOCAMPUS [LOPHOBANCHII]. By K. M. KADAM
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(Communicated by Sir Gavin de Beer, F.R.S. P.P.L.S.).

(With Plate 10 and 10 text-figures.)

[7 November 1957].

INTRODUCTION.

Our knowledge of the development of the skull in Lophobranchii is limited to that of the pipe-fish *Syngnathus* (McMurrich, 1883; Kindred, 1921, 1924). While McMurrich has given a general account of the chondrocranium of *Syngnathus peckianus*, Kindred gives a detailed description of that of *Syngnathus fuscus*. Ryder's account (1881) of the cranial morphology of *Hippocampus antiquorum* is meagre and the terminologies used by him are now obsolete. Swinnerton (1902) has made references to certain aspects of the skull of *Syngnathus* in his paper on *Gasterosteus* which is a generalized member of Gasterosteiformes of which Lophobranchii forms a suborder.

The form of body of the sea-horse, *Hippocampus* is unique, the head being bent at an acute angle to the vertical trunk. Though the curious shape of the head resembling that of a horse has attracted attention, very little is known about how this shape of the skull is derived. In order to investigate the peculiarities in the cranial morphology, the study of the development of the sea-horse was undertaken at the suggestion of Dr. L. S. Ramaswami. In this paper I propose to describe the chondrocranium and the osteocranium will be described at a future date.

MATERIAL AND METHODS.

The embryos were collected from the brood pouches of the male fish which were preserved in formalin. Some material was given to me by Dr. L. S. Ramaswami from his personal collections. A few advanced stages were secured from Taraporewala aquarium, Bombay. These were found outside the brood pouches and swimming in the aquarium. The advanced stages were decalcified in 1 per cent nitric acid in 70 per cent alcohol. Serial sections were cut 10 micra thick and stained in iron haematoxylin or Mallory's tripple stain.

Wax model reconstructions of 9mm., 12mm., and 18mm. (total length) stages were made from the serial sections which have been used for the description of this paper. The drawings of the chondrocranium have been made with the help of the wax models and checked with the transverse and sagittal sections.

OBSERVATIONS.

Stage 1 : 9mm. embryo (total length). (Figs 1, 2.)

The Basal Plate and Notochord.

The basal plate is traversed in its posterior two-thirds by the notochord (Fig. 1, NC). The tip of the notochord projects anteriorly into a small basicranial fenestra (BC) which is filled with cellular tissue. Though the basicranial fenestra extends posteriorly, it is only virtual as the space between the parachordals is occupied completely by the notochord. In front of the basicranial fenestra the parachordals are united by their mesial edges but have not completely fused. Their ventromesial edges are quite apart enclosing a groove in which the ossification of the parasphenoid is noticed. Behind the hypophysial fenestra (HF) the parachordals are interconnected

by the cartilaginous pro-otic bridge. This bridge gradually narrows posteriorly and disappears as the parachordals come together as mentioned above. In *Syngnathus* (Kindred, 1921) the parachordals are separated throughout their length by the notochord and a pro-otic bridge connects them at a later stage (43 mm. ; Kindred, 1924). In *Gasterosteus* (Swinnerton, 1902) the parachordals are fused together dorsally to the tip of the notochord forming a pro-otic bridge.

The basal plate is connected to the auditory capsule on each side by means of an extensive anterior basicapsular commissure (Fig. 1, ABC) posterior to the trigemino-

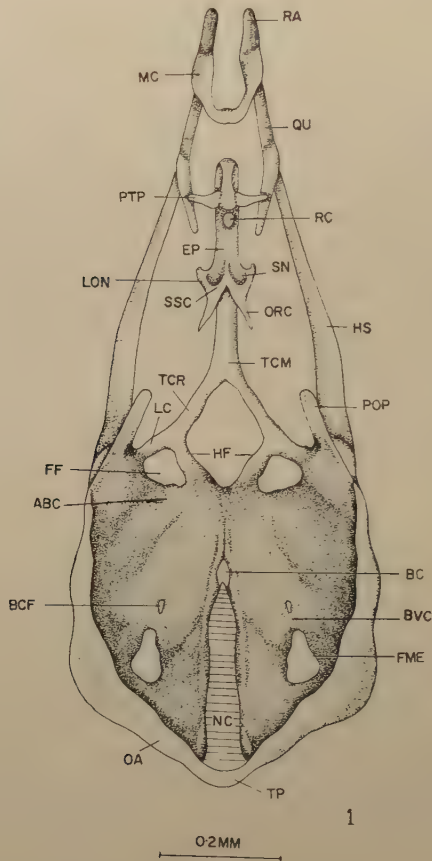


FIG. 1.—Dorsal aspect of the chondrocranium of *Hippocampus* (model). Embryo 9mm. long. Hyobranchial apparatus and taenia tecti medialis are not shown.

facialis chamber. The commissural cartilage is very broad as the basicapsular fenestra (BCF) is minute. The latter is bounded behind by a narrow basivestibular commissure (BVC). The metotic foramen (FME) is a wide fenestra lying between the occipital arch and the basivestibular commissure.

The notochord varies in thickness as well as in position during its course in the basal plate. Anteriorly it is more dorsal to the basal plate and is pear-shaped in cross-section. The broad dorsal part lies well above the dorsal surface of the basal plate while its narrow ventral part lies between the dorsomesial edges of the basal plate. In the middle region, the ventral half of the notochord gradually increases

in thickness and comes to lie between the parachordals, being adpressed by them. The ventral surface of the notochord is flat in this region and the dorsal surface continues to be arched or rounded. As the notochord approaches the occipital region it increases enormously in thickness—particularly the ventral half. The dorsal surface of the notochord and the basal plate are in the same plane, as the former does not extend above the dorsal surface of the latter. The mesial edges of the basal plate abut against the dorsolateral surfaces of the notochord. The ventral part of the notochord extends below the basal plate and the ventromesial edges of the parachordals are widely separated from one another. In the occipital region the notochord is bent sharply downwards because of the cranial flexure. The intracranial part of the notochord is, therefore, at right angles to the postcranial part.

The Occipital Region

The occipital arch (Fig. 1, OA) has fused with the posterior part of the parachordals and the hind wall of the auditory capsule. The occipital processes lie on the dorso-lateral surface of the notochord. They rise above the notochord dorsoposteriorly and as the notochord bends down they meet dorsally to the foramen magnum forming a narrow tectum posterius (TP). In *Syngnathus* (Kindred, 1921) the occipital processes are not connected by a tectum posterius in the 12mm. stage. In the same fish the occipital cartilage has fused with the posterior wall of the otic capsule enclosing a canal for the passage of the glossopharyngeal and vagus nerves. A similar canal is also noticed in the 6 mm. stage of *Gasterosteus* (Swinnerton, 1902). In *Hippocampus* the occipital arch, the basal plate and the hind wall of the otic capsule have fused forming the posterior boundary to the large metotic foramen. The IX and X cranial nerves pass out through this foramen and the canal referred to above is therefore not formed in the sea-horse.

The Auditory Region.

There is no cartilaginous medial wall to the otic capsule as in many teleosts. The roofing cartilage or tectum synoticum which connects the two otic capsules dorsally to the brain is also absent. But a small isolated median cartilage is present in the roof of the cranial cavity. This cartilage is the vestigial taenia tecti medialis (Fig. 2, TTM). In the 8-mm. stage of *Syngnathus* (Kindred, 1921) a narrow tectum synoticum is present in an exceptionally anterior position. In a corresponding stage (9 mm.) of *Gasterosteus* (Swinnerton, 1902) and *Gambusia* (Ramaswami, 1945) the tectum synoticum is broad and extends into the posterior part of the auditory region.

From the anterodorsal surface of the otic capsule an obliquely vertical process—the postorbital process (Figs 1, 2, POP)—is given off which projects into the posterior part of the orbit. It forms a side wall to the cranial cavity in that region. A prominent ridge extends posteriorly for a short distance from the lateral surface of the root of the postorbital process. The dorsal end of the hyosymplectic cartilage (Fig. 2, HS) articulates with the auditory capsule ventromesially to this ridge which may be called the speno-pterotoc ridge (Fig. 2, SPR).

The lateral wall of the otic capsule rises high in the middle region and slopes posteriorly. The external surface of the auditory capsule does not show grooves or swellings to reflect the position of the semicircular canals. But posteriorly the auditory capsule shows a large swelling laterally to accommodate the sacculus. Internally the cartilaginous septa of the semicircular canals are not well developed. The anterior septum is totally absent and the lateral septum is indicated by a slight projection on the inner surface of the capsular wall. Fibrous tissue extends from this ridge towards the lateral wall of the cranial cavity and forms the rudimentary septum semicirculare laterale. A similar but much broader ridge in the posterior region is the rudiment of the septum semicircularis posterius.

A ventromesial edge of the otic capsule has fused with the basal plate behind the exit of the facial nerve by a wide anterior basicapsular commissure as already mentioned. There is no posterior basicapsular commissure as the glossopharyngeal and vagus nerves emerge through a single metotic foramen.

The Orbito-temporal Region.

The anterior ends of the parachordals are fused with the posterior ends of the trabeculae cranii (Fig. 1, TCR) enclosing between them a wide fenestra myodomeus ventralis described by Kindred (1921) and by Allis (1919) in *Syngnathus*. De Beer (1937) calls it the hypophysial fenestra and the hypophysis is lodged in the posterior part of this fenestra. In the anterior part the recti eye-muscles pass mesially to the trabeculae and are inserted on the parasphenoid. The trabecular rods converge anterior to the hypophysial fenestra and fuse to form trabecula communis (Figs 1, 2, TCM) which is situated at a higher level than the basal plate.

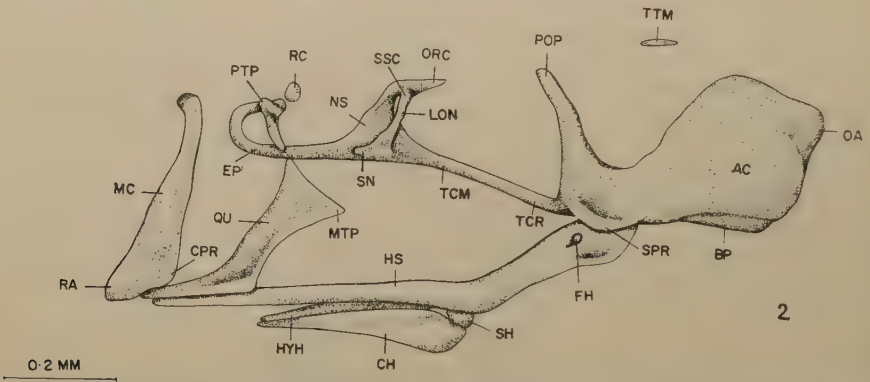


FIG. 2.—Lateral aspect of the chondrocranium of *Hippocampus* (model). Embryo 9 mm. long. Branchial skeleton is not shown.

From the ventromesial surface of the postorbital process a cartilaginous process connects the anterolateral edge of the parachordals and the trabecula cranii forming a lateral commissure (Fig. 1, LC). Between the lateral commissure and the anterior margin of the auditory capsule (anterior basicapsular commissure) a wide foramen (FF) is enclosed which forms the exit for the jugular vein and the hyomandibular branch of the facial nerve from the cranial cavity. In front of and dorsal to the lateral commissure there is deep indentation on the inner surface of the root of the postorbital process. A similar groove has been called incisum prooticum by Gaupp (1906) in *Salmo*. The jugular vein and the trigeminal nerve lie in this groove.

The trabecula communis (Figs 1, 2, TCM) formed by the fusion of the trabeculae cranii is a narrow elongated rod forming an interorbital septum together with a membranous septum which extends vertically from its dorsal part to the floor of the cranial cavity. In the posterior region of the orbit the membranous septum is low as the brain increases in size and lies closer to the trabecula communis. In the anterior region of the orbit there are two small cartilaginous rods lying one on either side of the fore-brain. These are the much reduced orbital cartilages which extend back from the posterior face of the lamina orbitonasalis (LON).

There is no epiphysial bar or any other roofing cartilage in this region.

The Ethmoid Region.

The trabecula communis broadens slightly into the ethmoid plate (Fig. 1, EP) in the nasal region. It is very much elongated and rod-like extending in front of

the nasal region. The anterior half of the pre-nasal part of the ethmoid plate is curiously bent upwards and backwards on itself in the form of an arch. The dorsal and backwardly directed region is narrower than the ventral broader part. A transverse section in this region (Fig. 8), therefore, shows two distinct portions of the ethmoid plate (EP) one below the other. The actual anterior end of the ethmoid plate is directed posteriorly and lies dorsally to the horizontal part. It is slightly broadened dorsolaterally to form the pre-ethmoid cornua with which the pterygoid process of the quadrate (Figs 1, 2, 8, PTP) is fused. The connection between the two is procartilaginous as seen in the 5mm. stage of *Gasterosteus* (Swinerton, 1902).

A large rostral cartilage (Figs 1, 2, RC) lies dorsal to the anterior end of the ethmoid plate. The cartilage occupies an unusually dorsoposterior position due to the bending of the ethmoid plate.

A median dorsal ridge on the ethmoid plate between the nasal sacs forms the nasal septum (Figs 1, 2; Pl. 10, fig. 11, NS). The nasal septum gradually increases in its height posteriorly. The dorsal edge of the septum is thicker than its middle part in the posterior region. The ventral edge of the nasal septum is broad and is fused with the ethmoid plate. The two cartilages however retain their identity. Histologically the nasal septum consists of smaller cartilage cells and less of matrix than the ethmoid plate (EP) which has larger and fewer cells and greater matrix and the perichondrium separating the two cartilages at the region of their fusion is clearly seen in transverse sections (Pl. 10, fig. 11). The nasal septum probably appears later than the ethmoid plate as an independent chondrification during the early development of the chondrocranium. In the posterior region of the nasal sac the ventral edge of the nasal septum forms a wing-like expansion—the solum nasi—(Figs 1, 2; Pl. 10, fig. 11, SN) which forms the floor of the olfactory sac in that region. The posterolateral edge of the solum nasi is connected with the ventral edge of the lamina orbitonasalis (Figs 1, 2, LON) which is a vertical rod of cartilage forming the posterior boundary to the nasal sac. The dorsal edge of the lamina orbitonasalis is connected with the nasal septum by means of a short sphenoseptal commissure (ssc). The olfactory nerve passes through the foramen olfactorium advehens which is bounded laterally by the lamina orbitonasalis, mesially by the nasal septum and dorsally by the sphenoseptal commissure.

The cartilaginous nasal septum is continuous behind with the membranous interorbital septum. The oblique eye muscles are attached to the anterior region of the interorbital septum just behind the nasal septum.

From the posterodorsal end of the lamina orbitonasalis a small cartilaginous rod projects backwards into the orbit. This is the vestige of the poorly developed orbital cartilage (Figs 1, 2, ORC). In *Syngnathus* (Kindred, 1921) the orbital cartilage is very much reduced as in *Hippocampus*.

The Visceral Arch Skeleton.

The pterygoquadrate bar of cartilage is divided into a dorsal small pterygoid process of the quadrate (Figs 1, 2, PTP) and a large ventral quadrate proper (QU). In a slightly earlier stage it is observed that the two parts of the pterygoquadrate cartilage are continuous by means of a slender cartilaginous connection. The dorsal part of the pterygoid process is broad and shows a rostralpalatine process which is in procartilaginous connection with the pre-ethmoid cornu of the ethmoid plate. As there is no ethmopalatine connection the articulation of the palatoquadrate with the ethmoid region is of the "acartete" type (Swinerton, 1902) as in *Gasterosteus* (Swinerton, 1902) and *Syngnathus* (Kindred, 1921).

The quadrate in *Hippocampus* has an anteroventral limb articulating with Meckel's cartilage and a large plate-like vertical limb lying in the side wall of the oral chamber in front of the nasal region. The anterior articular tip of the quadrate is fused with the under surface of Meckel's cartilage, but this appears to be in the process of

disappearing. In the 10mm. stage of *Clupea* (Wells, 1922) Meckel's cartilage and the quadrate are continuous and they become separated in the 30mm. stage.

The vertical part of the quadrate shows a small process in the middle of its posterior border. This is the reduced metapterygoid process (Fig. 2, MTP) which is longer in *Syngnathus* (Kindred, 1921) projecting up to the middle region of the orbit.

Meckel's cartilages (Figs 1, 2, MC) are peculiar in that they lie vertically and are tilted a little backwards so that their anterior ends lie dorsally and posteriorly just in front of the bend of the ethmoid plate. The two rami of Meckel's cartilages are fused at the symphysis. In front of the articular region the cartilage is thicker than in its ventral part. The part of the cartilage which lies in front of the quadrate-articular joint in this stage is the retroarticular process (Figs 1, 2, RA). By subsequent movement and growth it lies behind and below the articular region in later stages as in other teleosts. Dorsally to this region there is a coronoid process (Fig. 2, CPR) which is not well developed.

In the hyoid arch, the hyosymplectic cartilage (Fig. 2, HS) is highly elongated, extending in front up to the lower jaw and articulating with the auditory capsule behind. The anterior half of the hyosymplectic is rod-like and lies at an obtuse angle to the posterior plate-like part. The anterior region of the hyosymplectic underlies almost the complete length of the quadrate. The posterodorsal articular surface of the hyomandibular is elongated and lies in a groove on the ventrolateral surface of the auditory capsule. Lateral to the articular surface there is a prominent ridge (parotic ridge of Norman, 1922) to which reference has already been made.

The hyomandibular branch of the facial nerve (Fig. 2, FH) pierces through the hyomandibular cartilage just anterior to its articulation with the auditory capsule as seen in *Syngnathus* (Kindred, 1921) and *Gasterosteus* (Swinerton, 1902).

The hyosymplectic cartilage is independent of the pterygoquadrate in *Hippocampus*. In *Syngnathus* (Kindred, 1921) the distal end of the symplectic is confluent with the pterygoquadrate in the 8mm. embryo and becomes separated later. In *Clupea* (Wells, 1922) and *Ophicephalus* (Srinivasachar, 1953) the proximal ends of the symplectic and quadrate are fused with the hyomandibula.

The hypohyal (Figs 2, 3, HYH) and ceratohyal (CH) are elongated rods narrow anteriorly and broad posteriorly. The hypohyals lie on the inner surface of the ceratohyals and their anterior ends meet in the middle line while posteriorly they are separated and are attached to the copula communis (Fig. 3, CC). The ceratohyal is connected posterodorsally with the hyosymplectic cartilage through a small stylohyal cartilage (SH).

The Branchial Arches (Fig. 3).

The copula communis (CC) is an elongated cartilaginous rod pointed at both ends. It is thickest where the posterior ends of the hypohyals are attached. In the anterior region the copula is dorsal to and well separated from the hypohyals and ceratohyals. Posteriorly it extends to the second branchial arch. The first branchial arch (BR 1) starts above the posterior region of the copula communis and extends horizontally for a short distance and rises gradually towards the dorsal region of the pharynx. The epibranchials (EBR 1, EBR 2) and the pharyngobranchials (PBR 1-2) are differentiated in the first and second branchial arches. The epibranchials are connected mesially to the pharyngobranchials 1 and 2. The cartilages of the second arch meet ventrally in the middle line just posterior to the tip of the copula communis. The hypobranchials are not distinguishable from the ceratobranchials and the entire arch is in the form of a bent rod of cartilage. In the third, fourth and fifth branchial arches the epi- and pharyngobranchials are not differentiated. The ventral ends of each of these arches meet in the middle line as there are no basibranchial elements in these arches. In the 8mm. stage of *Syngnathus* (Kindred, 1921) a core of pro-cartilaginous cells extends from the posterior end of the copula communis and in the 12mm. stage distinct basibranchials are present in the branchial arches. The fifth

arch which is not developed in the 8mm. stage of *Syngnathus* appears as short cartilages in the 12mm. stage.

On either side of the symphyseal region of Meckel's cartilages there is a pair of densely cellular masses in a membranous fold. These represent the infralabial cartilages.

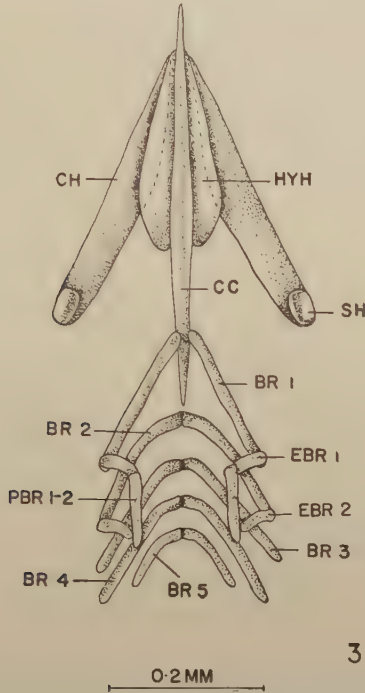


FIG. 3.—Dorsal aspect of the hyobranchial skeleton of *Hippocampus* (model). Embryo 9mm. long.

Stage 2 : 12mm. embryo (total length). (Fig. 4.)

The ethmoid plate in front of the nasal sacs which was bent on itself in the previous stage is in the process of straightening. The anterior half of the plate has lost its backward bend and lies almost at right angle to the horizontal part. In this stage the ethmoid plate is very similar to the condition seen in the 8mm. stage of *Syngnathus* (Kindred, 1921). The anterior distal end is much broader than in the previous stage as the pre-ethmoid cornua are well chondrified and they are in cartilaginous continuity with the pterygoid processes of the quadrate. On the ventral aspect of the posterior half of the ethmoid plate there is a median groove in which the ossification of the vomer is observed. The nasal septum has grown thicker especially in its dorsal edge. The membranous portion lying in the posterior region has also chondrified and hence the posterior extent of the nasal septum is greater than in the previous stage. Due to the growth of cartilage in the posterior dorsal region of the nasal septum the sphenoseptal commissure is very short.

The trabecula communis has broken down and is disconnected from the parachordals as in 24mm. stage of *Ophicephalus* (Srinivasachar, 1953). In *Gambusia* (Ramaswami, 1945) the connection is absent in as early as 5mm. embryo. In the corresponding stage of *Syngnathus* (12mm., Kindred, 1921) the trabeculae are continuous and the discontinuity is noticed in a 43mm. specimen (Kindred, 1924).

The minute basicapsular fenestra has disappeared as the metotic foramen has extended anteriorly by the disappearance of the basivestibular commissure. In *Syngnathus* Kindred (1921) described a similar small foramen in the 8 and 12mm. stages. In the 43mm. stage the fenestra is large and is closed by a bony plate.

The membranous labyrinth has increased in size and the otic capsule is more expanded laterally in the posterior region.

The taenia tecti medialis has grown slightly and is longer and stouter than in the previous stage.

Considerable changes have occurred in the visceral arch skeleton. The pterygoquadrate has distinctly broken down into an anterior pterygoid process and a posterior quadrate. The discontinuity is greater than in the 9 mm. stage. The

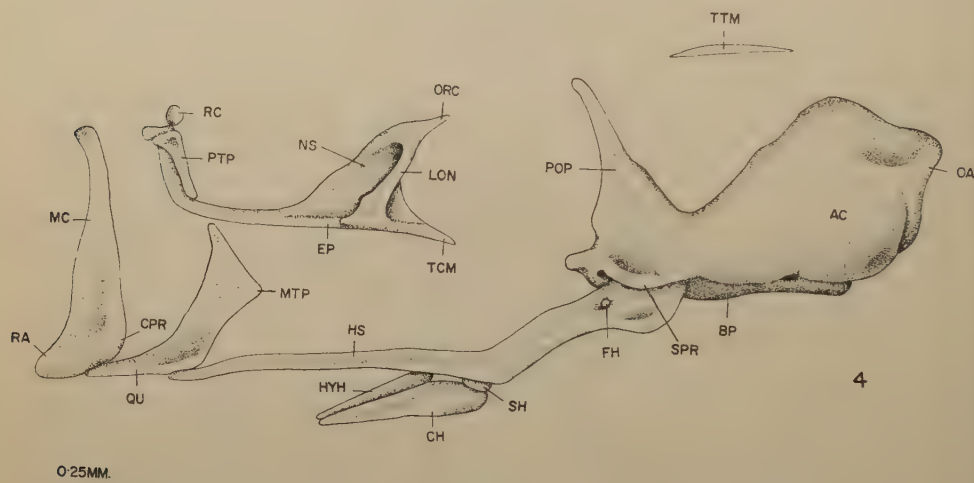


FIG. 4.—Lateral aspect of the chondrocranium of *Hippocampus* (model). Embryo 12 mm. long. Branchial skeleton omitted.

pterygoid process is partially fused with the under surface of the pre-ethmoid cornu as in 9mm. stage of *Gasterosteus* (Swinnerton, 1902). It lies in an oblique position due to the straightening and elongation of the ethmoid plate. The quadrate has moved forwards and lies in front of the nasal region. The narrow cartilaginous connection between the quadrate and Meckel's cartilage seen in the previous stage at the articular joint is lost.

Meckel's cartilages are vertical but are slanting forwards from the backwardly directed position seen in the previous stage. The coronoid process is well developed and lies dorsal to the articular region. The retroarticular process is anterior to the articular region as in the previous stage. The two rami of the lower jaw are separate at the symphysis.

The anterior portion of the hyosymplectic cartilage, which extended almost the whole length of the quadrate in the earlier stage, now lies at the posterior end of it. The symplectic cartilage is broader where it is confluent with the hyomandibular part. The stylohyal connects the hyomandibular and the ceratohyal in this region. A change in the position of the segments of the hyoid arch is noticed due to the widening of the oral cavity. The copula communis has moved down ventrally carrying the hypophyals and the ceratohyals with it. Both the cartilages lie in an oblique position instead of the horizontal plane and are not as long as in the 9mm. stage. Their anterior ends are separated from the copula communis. The posterior end of

the hypohyal articulates with the copula communis while the ceratohyal articulates with the hyomandibula through the stylohyal.

In the first and second branchial arches the pharyngobranchials are present in a fused condition as before. The epibranchials are separate and they have appeared in the third branchial arch also. The fourth branchial arch has grown further and extends beyond the fifth branchial arch. There are no basibranchials in the last three arches. In *Syngnathus* (Kindred, 1921) there are independent basibranchial cartilages in the third and fourth arches in the 12mm. stage.

The straightening of the ethmoid plate has brought about a change in the position of the rostral cartilage (Fig. 4, RC). It is now larger and lies dorsally on the posterior border of the anterior end of the ethmoid plate. The premaxillary and maxillary ossifications have appeared as thin bony laminae articulating with the rostral cartilage.

The cellular masses representing the infralabial cartilages are bigger and consist of closely packed clusters of cells lying on either side of the symphysial region of the lower jaw.

*Stage 3 : 18 mm. embryo (total length). Fully formed
chondrocranium. (Figs 5, 6.)*

Most of the cartilages have reached their maximum development and the chondrocranium of this stage may be described as being fully formed.

The growth of the ethmoid region is marked by the elongation and straightening of the anterior region. The upward bend is lost and the distal part is broad with the well developed pre-ethmoid cornua (Fig. 5 EC). Behind this region the ethmoid plate is narrow and is circular in cross-section. In front of the nasal region it is broader, thin and plate-like. The growth of cartilage is pronounced in the nasal region. The nasal septum is massive and the fusion of its ventral edge with the ethmoid plate is greater than in the previous stages. However, the original extent of the two cartilages can be made out in cross-sections (Pl. 1, fig. 12). The lamina orbitonasalis is stouter and vertical, attached ventrally to the dorsolateral edge of the solum nasi and dorsally to the dorsolateral edge of the nasal septum. The cartilage is thick and massive in this region of the fusion of the lamina orbitonasalis with the nasal septum, and the slender sphenoseptal commissure observed in the earlier stages is obliterated. Posteriorly, from the dorsal edge of the nasal septum the short orbital cartilages project into the orbit.

The trabecula communis is discontinuous as in the previous stage and extends posteriorly for a short distance from the ethmoid plate. The membranous inter-orbital septum is inserted on to its dorsal surface anteriorly and in the posterior region it is attached to the parasphenoid bone. The orbital cartilages extending from the lamina orbitonasalis are a little longer than in the 12mm. stage.

The myodome is deep and well formed in the 18mm. stage. The posterior extent of the myodome does not reach the ventral part of the basis cranii as described by Allis (1919) in *Hippocampus guttulatus* since the parasphenoid lies closely applied to the ventral surface of the basal plate. The recti externi muscles are attached to the dorsal surface of the parasphenoid which forms the floor of the myodome. The lateral wall is formed by the mesial edge of the trabeculae and the roof by the membrane of the cavum cerebrale cranii. In other respects the myodome conforms with the description of Allis (1919).

The deep notch on the anterior surface of the root of the postorbital process seen in the earlier stages is converted into a foramen by the growth of a short cartilage, the pila lateralis (Fig. 5, PL), connecting the base of the postorbital process (POP) and the trabecula. The branches of the trigeminal nerve pass through this foramen (FTR). A similar foramen develops in the 43mm. stage of *Syngnathus* (Kindred, 1924) by a downward growth of "alisphenoid pedicel" from the postorbital process.

On the lateral surface of the postorbital process there is a prominent ridge also

observed in the earlier stages. The hyomandibular cartilage articulates ventromesially to this ridge with the auditory capsule. The articular surface of the hyomandibula does not extend into the region of the capsule containing the membranous labyrinth. According to Allis (1919a) a similar ridge in *Lepidosteus* is called the

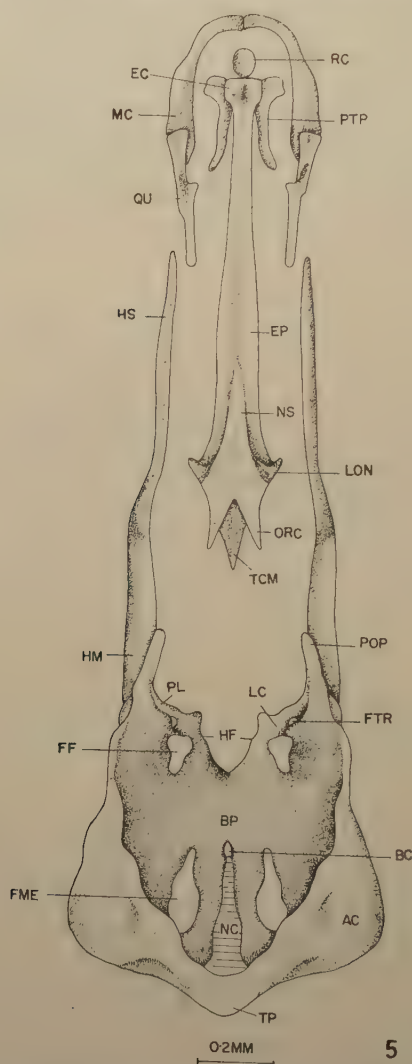


FIG. 5.—Dorsal aspect of the chondrocranium of *Hippocampus* (model). Embryo 18mm. long (fully formed chondrocranium). Taenia tecti medialis and hyobranchial skeleton are not shown.

“spheno-pterotic ridge”. The ridge extends on the lateral surface of the prominence of the lateral semicircular canal in *Lepidosteus* (Allis, 1919a) and *Amia* (Pehrson, 1922) but in *Hippocampus* as the hyomandibula articulates in front of the lateral semicircular region, the spheno-pterotic ridge is short and less extensive.

The cartilaginous septa of the lateral and posterior semicircular canals in the auditory capsule remain only as broad ridges and are not completely developed. The auditory capsule does not show external prominences of the semicircular canals.

In the roof of the cranial cavity the taenia tecti medialis (Fig. 6, TTM) has grown further. The anterior end of this cartilage is thin and plate-like and posteriorly it is in the form of a cylindrical rod. Even in this stage the cartilage is independent and vestigial. It is the only roofing cartilage in the neurocranium.

The notochord lies in a more posterior position leaving a small basiscranial fenestra which is filled with cellular tissue. In the posterior region the notochord is very thick. The occipital arches project from the dorsolateral surface of the notochord and are fused dorsally forming the tectum posterius (Fig. 5, TP). The tectum projects for a short distance posteriorly. The first pair of spinal nerves emerge just posterior to the occipital arch.

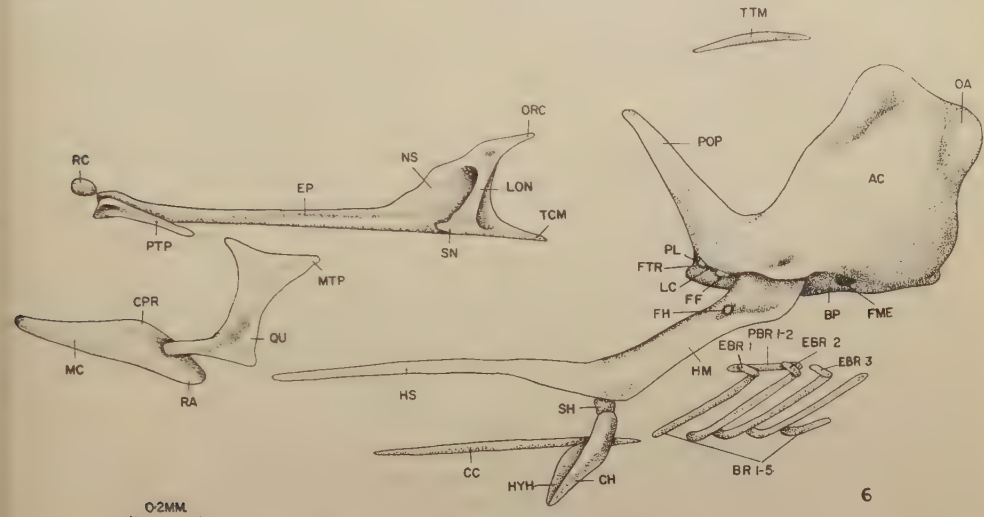


FIG. 6.—Lateral aspect of the chondrocranium of *Hippocampus* (model). Embryo 18mm. long (fully formed chondrocranium).

Due to the complete straightening of the ethmoid plate the pterygoid process of the quadrate has assumed a horizontal position and lies on either side of the straightened anterior region of the ethmoid plate. Distally the pterygoid process articulates with the lower surface of the pre-ethmoid cornu. The cartilaginous connection existing between the pterygoid process and the ethmoid plate in the 12mm. stage is lost and the two cartilages are separate (Fig. 9). Though the pterygoid processes have grown longer they are not nearer to the quadrate whereas in *Syngnathus* (Kindred, 1921) the cartilages are in close proximity in advanced embryos.

The quadrate (Figs 5, 6, QU) articulates with the posterodorsal surface of Meckel's cartilage which is now in an almost horizontal position. The articular tip of the quadrate is broad and flat while posteriorly the cartilage is rounded. The vertical limb is plate-like and shows two processes dorsally. The anterior of the two is directed towards the pterygoid process and the posterior is the metapterygoid process (Fig. 6, MTP). The quadrate is carried further anteriorly and lies well in front of the nasal region.

Meckel's cartilages have undergone a complete rotation from their earlier vertical position and are almost horizontal. The retroarticular process extends posteriorly below the quadrate. The quadrate articulates with the dorsal surface of the retroarticular process instead of the previous posterior articulation. The coronoid process which is dorsal to the articular surface in the previous stages now lies in front of it. The dentary ossification has appeared flanking Meckel's cartilage.

The large cellular masses representing the unchondrified infralabial cartilages observed in the earlier stages are present in a reduced condition.

The symplectic part of the hyosymplectic cartilage is slender and horizontal. It does not extend, as it did in the previous stage, ventrally to the quadrate but now lies behind it. The symplectic cartilage gradually becomes thicker as it merges with the hyomandibular part. The stylohyal articulates on the inner surface of the hyomandibula. The articular head of the hyomandibula lies in a groove of the auditory capsule overhung by the sphenopterotic ridge. The hyomandibular branch of the facial nerve passes through a foramen in the hyomandibular cartilage and in this region the cartilage is narrower than in the previous stages.

The hypohyal and ceratohyal cartilages have also undergone a change in their position from the horizontal plane to the vertical and are also diminished in size. Their anterior ends which were nearer to the copula communis are widely separated now from it. Posteriorly the hypohyal is attached to the copula communis and the ceratohyal to the stylohyal.

The copula communis which in the 12mm. stage extended up to the second branchial arch, in the 18mm. stage ends in front of the first branchial arch. The branchial arches are well formed and consist of bent cartilages. Except for the first branchial arch the remaining arches meet ventrally in the middle line as the basibranchial cartilages are absent. The ventral ends of the first arch are separated and lie dorsally to the copula communis.

The pharyngobranchials of the first and second branchial arches are continuous and are connected laterally to their respective epibranchials. In the third branchial arch a separate epibranchial (Fig. 6, EBR 3) has appeared. The fifth branchial arch is slightly longer than in the previous stage. It lies more or less in a horizontal position.

The rostral cartilage lies in front of the ethmoid plate with which it comes in contact by its posterior border.

The sclerotic cartilages are present in all stages in the eye-ball as shallow ring-like cartilages in the region of the greatest diameter of the eye ball.

DISCUSSION.

The ethmoid region of *Hippocampus* is the most strikingly specialized part of the chondrocranium. In the fully formed stage (18mm. embryo) it is elongated to an unprecedented degree, found in a few other teleosts like *Syngnathus* (Kindred, 1921, 1924) where it is to a lesser extent.* The anterior half of the ethmoid plate which is bent on itself in stage 1 of *Hippocampus* gradually straightens with the development of the embryo. An intermediate condition in the process of straightening is noticed in the 12mm. embryo where the anterior part is almost at right angle to the posterior horizontal part. An identical stage is seen in the 8mm. embryo of *Syngnathus* (Kindred, 1921). In the earlier stages of the pipe-fish Kindred has not recorded any backward bend of the ethmoid region. In an allied genus *Siphonostoma* Norman (1926, p. 402) stated that he found "no trace of this phenomenon, nor any thing analogous to it" in the embryos ranging from 9 to 15 mm. in length. The curious backward bend of the ethmoid plate in *Hippocampus* is perhaps to be interpreted as an embryonic adaptation of the embryo to develop inside the brood pouch where a need for economy of space is felt. This conclusion is borne out by the fact that the ethmoid plate straightens in the embryos that have emerged from the brood pouch.

The rotation of Meckel's cartilages may also be considered here as a necessary consequence of the above mentioned phenomenon. Meckel's cartilages in the early stages are not only vertical but also slant backwards so that the morphological

* Also in certain Mormyridae and deep-sea eels.

anterior end is dorsal and posterior to their retroarticular processes which are ventral and anterior. The retroarticular process lies in front of the quadrate-articular joint. In the fully formed chondrocranium the disposition is quite reversed, brought about by the rotation of the cartilages by about 90 degrees. They are horizontal with the retroarticular process lying behind and below the articular joint. The articular tip of the quadrate provides the fulcrum for the rotation of the mandible.

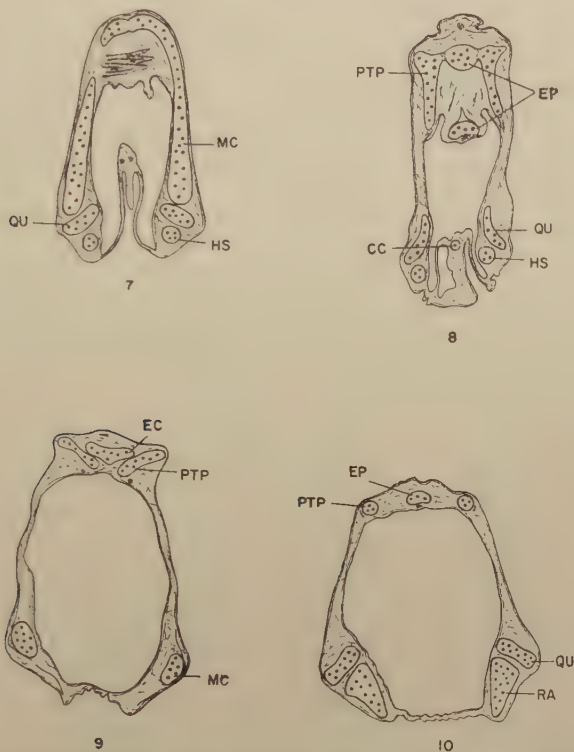


FIG. 7.—Transverse section of the 9mm. embryo (total length) of *Hippocampus* in front of the ethmoid plate showing the vertical nature of Meckel's cartilages and their dorsal symphysis. $\times 80$.

FIG. 8.—Transverse section of the anterior ethmoid region of the 9mm. embryo (total length) of *Hippocampus* showing the fusion of the pterygoid process of the quadrate with the pre-ethmoid cornu. $\times 80$.

FIG. 9.—Transverse section of the 18mm. embryo (total length) of *Hippocampus* through the same region as that of Fig. 8. $\times 40$.

FIG. 10.—Transverse section of the 18mm. embryo (total length) of *Hippocampus* at the quadrate-lower jaw articulation. $\times 40$.

In *Syngnathus* (Kindred, 1921) where the bending of the ethmoid plate is observed, Meckel's cartilages show a peculiar condition. In the 8mm. stage Meckel's cartilage is deeply curved on its ventral surface. The concavity becomes obliterated and the mandible is straightened in the 12mm. embryo correlated with the straightening of the ethmoid plate.

The nasal region of the chondrocranium of Syngnathidae is of interest as it exhibits a somewhat specialized condition. Generally in teleosts the ethmoid plate gives rise to a median vertical cartilage, the septum nasi (mesethmoid cartilage), separating the two nasal sacs. In the posterior region the lateral edges of the ethmoid plate

give rise to the laminae orbitonasales (ectethmoid cartilages) which form the posterior walls of the nasal capsules. In *Syngnathus* (Kindred, 1921) the laminae orbitonasales arise independently of the ethmoid plate. They are in the form of narrow vertical rods of cartilage lying ventral to the anterior end of the brain. Later these cartilages become connected with one another dorsally forming a horse-shoe shaped arch, the ectethmoid arch of Kindred. Norman (1926, p. 406) states that they never become fully connected with the ethmoid plate. But in a 43mm. stage of *Syngnathus* Kindred (1924, p. 434) describes the formation of a massive internasal septum "by the fusion of the paired ectethmoid cartilages with each other mesially and with the ethmoid plate ventrally". In *Siphonostoma* Norman (1926) observes that in the early stages the ectethmoid cartilages appear as independent procartilaginous masses and even at an advanced stage they remain separate from the ethmoid plate and are not completely chondrified. He concludes that "their independence of the ethmoid plate in such specialized forms as the Syngnathids seems to be of little importance and is almost certainly a secondary condition".

In *Hippocampus* the laminae orbitonasales are noticed to be attached to the ethmoid plate quite early. They are also attached to the nasal septum. But it may safely be stated that as in *Syngnathus* and *Siphonostoma* these cartilages have arisen independently of the ethmoid plate, because of their histological difference with the older ethmoid plate and also because of the persistence of the perichondrial membrane between the two throughout their development. In *Cyclopterus* (Uhlmann, 1921) also the ectethmoid cartilages chondrify independently and do not arise as outgrowths of the ethmoid plate.

The pterygoquadrate chondrifies as a continuous bar of cartilage in many teleosts like *Gasterosteus* (Swinnerton, 1902), *Amia* (Pehrson, 1922), *Gambusia* (Ramaswami, 1945). In forms such as *Clupea* (Wells, 1923) and *Ophicephalus* (Srinivasachar, 1953) the pterygoquadrate chondrifies in two parts, viz., the pterygoid process of the quadrate and the quadrate. They chondrify independently in early stages and later grow and become continuous into a single bar. In *Clupea* and *Ophicephalus* the continuity is again lost in advanced stages by the absorption of the cartilage in the middle of the bar. In *Amiurus* (Kindred, 1919), and other Siluroids (*Silonia*, *Pungasius*, *Ailia* : Srinivasachar, 1956) the pterygoquadrate bar is never complete at any stage of development. The two parts chondrify independently and remain separate. In *Salmo* and *Gadus* (de Beer, 1937) the pterygoid process arises as an anterior outgrowth of the quadrate. The process may not develop at all and may remain in a very rudimentary condition as in *Anguilla* (Norman, 1926). *Hippocampus* resembles *Ophicephalus* in possessing a slender cartilaginous continuity between the pterygoid process and the quadrate and again losing it as development proceeds. In *Syngnathus* (Kindred, 1921) the cartilaginous connection is represented by a fibrous connective tissue which connects the lower end of the pterygoid process with the upper anterior end of the quadrate.

The auditory capsule of *Hippocampus* does not show external indications of the semicircular canals. Kindred (1921) does not mention these prominences in *Syngnathus*. Internally, the anterior semicircular canal septum is absent in *Hippocampus* as in *Syngnathus* (Kindred, 1921), *Gambusia* (Ramaswami, 1945) and *Ophicephalus* (Srinivasachar, 1953). The septa of the lateral and posterior semicircular canals are not completely developed and they remain as broad ridges on the inner surface of the capsular wall in *Hippocampus*. Kindred (1921) also states that in the different stages of *Syngnathus* he has examined, the lateral and posterior semicircular septa are membranous and do not show chondrification. In *Hippocampus* as in *Syngnathus* and other Lophobranchii (Berg, 1940) the semicircular canals are short and broad and are hardly separated by any space from the utriculus.

The roofing cartilage in the auditory region of *Hippocampus* is reduced further when compared with that of *Syngnathus*. In the latter there is a slender tectum synoticum connecting the anterior region of the otic capsules. In *Hippocampus* the tectum

synoticum is totally absent. The roofing cartilage is represented by a slender rod of cartilage which is the remnant of the taenia tecti medialis. The only other roofing cartilage is the slender tectum posterius connecting the occipital processes.

In the branchial skeleton of *Hippocampus* the basibranchials do not make their appearance in any of the stages. In the early stages the copula communis extends to the second branchial arch. But in later stages it ends in front of the first branchial arch. All the branchial arches except the first meet ventrally in the middle line as there are no basibranchial elements in any of them. In the 12mm. stage of *Syngnathus* (Kindred, 1921) the basibranchials are present as small median cartilages in the third and fourth arches while in the first and second arches the copula communis lies in the midventral position. The basibranchials disappear and the copula communis ends in front of the second branchial arch in the 43 mm. specimen so that the second, third, fourth and fifth branchial arches meet ventrally in the middle line; a similar condition is also seen in the 18mm. stage of *Hippocampus*. Ryder (1881) has figured and described only four branchial arches in *Hippocampus antiquorum*. He has obviously missed the small fifth arch as his description is based on a whole mount.

SUMMARY.

1. Three stages in the development of the chondrocranium of *Hippocampus* are studied. In the last stage it is fully formed.

2. The ethmoid plate has an upward and backward bend in the 9mm. stage of *Hippocampus*. This flexure gradually straightens and the normal horizontal condition is assumed in the fully formed chondrocranium.

3. The lamina orbitonasalis and the nasal septum exhibit their independent origin from the ethmoid plate by retaining their identity even after fusing with the ethmoid plate.

4. The orbital cartilages are reduced and are in the form of a pair of short processes projecting back from the laminae orbitonasales.

5. The trabecula communis becomes disconnected from the basal plate in the 12mm. stage. It is present in the fully formed chondrocranium as a small posterior process of the ethmoid plate. Hence the ethmoid region of the chondrocranium is independent of the occipito-auditory region.

6. A pila lateralis develops in the 18mm. stage enclosing the trigeminal nerve. In the earlier stages there is only a groove, the incisivum pro-oticum.

7. A lateral commissure is completely developed forming the ventrolateral wall to the trigemino-facialis chamber.

8. There is a minute basicapsular fenestra in stage 1. It becomes confluent with the metotic foramen in later stages.

9. The otic capsule does not show external prominences of the semicircular canals. There are no complete cartilaginous septa separating the semicircular canals.

10. There is no tectum synoticum. A slender tectum posterius connects the two occipital processes.

11. A vestigial taenia tecti medialis is the only roofing cartilage in the chondrocranium.

12. The pterygoid process of the quadrate is vertical in the 9mm. stage and it assumes a horizontal position in the 18mm. stage. The process is continuous with the body of the quadrate by means of a thin cartilaginous extension in early stages. The two parts become separated as the ethmoid plate is straightened. The pterygoid process which is at first fused with the ethmoid plate articulates later by means of a distinct rostralpalatine process with the pre-ethmoid cornu conforming to the "acartete" condition of Swinnerton's description.

13. The quadrate in the 9mm. stage is fused with Meckel's cartilage and separates from it later.

14. Meckel's cartilages are obliquely situated in the early stages and undergo a rotation of about 90 degrees to assume a horizontal condition along with the straightening of the ethmoid plate.

15. The hyosymplectic cartilage is elongated and extends to Meckel's cartilage and lies below the quadrate in early stages. In later stages the anterior end of the hyosymplectic lies behind the quadrate. The hyomandibula articulates with the otic capsule in front of the region of the lateral semicircular canal. A spheno-pterotic ridge overhangs the articular facet.

16. The copula communis in the fully formed stage does not extend beyond the first branchial arch. There are no basibranchial elements in the branchial arches.

17. The hypohyal and ceratohyal are distinct cartilages and undergo a change in position and size during development.

18. A well developed rostral cartilage is present on the dorsal surface of the distal end of the ethmoid plate from the early stages. It also moves with the ethmoid plate to assume an anterior position.

19. Infralabial cartilages are present in the form of reduced dense cellular masses.

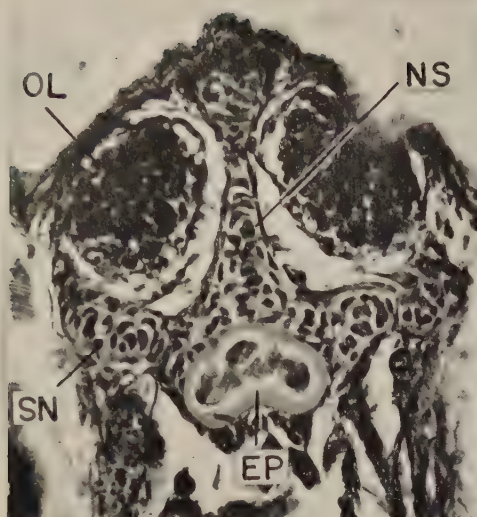
20. Sclerotic cartilages are present in the optic capsules.

ACKNOWLEDGMENTS.

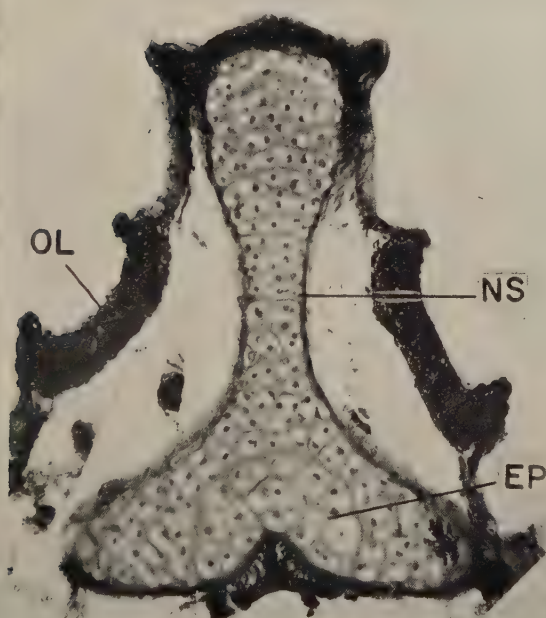
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11



12

EXPLANATION OF PLATE 10.

FIG. 11.—Photomicrograph of the transverse section of the nasal region of 9mm. embryo (total length) of *Hippocampus* showing the independence of the nasal septum from the ethmoid plate. $\times 300$.

FIG. 12.—Photomicrograph of the transverse section of the nasal region of 18mm. embryo (total length) of *Hippocampus*. $\times 300$.

KEY TO LETTERING OF ALL FIGURES.

ABC—anterior basicapsular commissure.	MC—Meckel's cartilage.
AC—auditory capsule.	MTP—metapterygoid process.
BC—basiscranial fenestra.	NC—notochord.
BCF—basicapsular fenestra.	NS—nasal septum.
BP—basal plate.	OA—occipital arch.
BR 1-5—branchial arches 1-5.	OL—olfactory sac.
CC—copula communis.	ORC—orbital cartilage.
CH—ceratohyal.	PBR 1-2—pharyngobranchials 1-2.
CPR—coronoid process.	PL—pila lateralis.
EBR 1-3.—epibranchials 1-3.	POP—postorbital process.
EC—pre-ethmoid cornu.	PTP—pterygoid process of the quadrate.
EP—ethmoid plate.	QU—quadrate.
FF—foramen for the hyomandibularis branch of facial nerve.	RA—retroarticular process.
FME—metotic foramen.	RC—rostral cartilage.
FTR—trigeminal foramen.	SH—stylohyal.
HF—hypophysial fenestra.	SN—solum nasi.
HM—hyomandibular cartilage.	SPR—spheno-pterotic ridge.
HS—hyosymplectic cartilage.	SSC—sphenoseptal commissure.
HYH—hypohyal.	TCM—trabecula communis.
LC—lateral commissure.	TCR—trabecula cranii.
LON—lamina orbitonasalis.	TTM—taenia tecti medialis.

CYATHOSTOMA LARI BLANCHARD, 1849 [NEMATODA, STRONGYLOIDEA]: ITS ANATOMY, INTRA-SPECIFIC VARIATION AND HOSTS, WITH A RE-DEFINITION OF THE GENUS. By D. R. R. BURT, F.L.S. and J. MARGARET EADIE,* Department of Natural History, University of St. Andrews, Fife.

(With Plate 11, 2 text-figures and 3 Tables.)

[Read 24 May, 1957.]

I. *Cyathostoma lari* Blanchard, 1849.

The genus *Cyathostoma* was created in 1849 by E. Blanchard to accommodate a nematode from the orbital cavity of the Black-headed Gull, *Larus ridibundus* L., taken in Sicily. This worm, which he named *Cyathostoma lari* is accordingly the genotype, and, in view of subsequent descriptions of other species referred to this genus it is unfortunate that the type is not more adequately defined. The original description of *C. lari* is that of the female, and little has been added to this description, but a male, known from an earlier record by von Siebold (1837) from a different host, the Lesser Black-backed Gull *Larus fuscus* L., has been considered to be the same species. In this latter account von Siebold records the host, the site of the parasite—*cella infraorbitalis*—within the host, the size and the possession by the male of a cauda bursa and he assigns the form to the genus *Strongylus*.

Chapin (1925), in his account of species of *Syngamus* and *Cyathostoma*, follows Leiper (1931) in his adoption of certain characters as having specific value, and he accepts the same characters, where such are applicable, in dealing with known and new species of *Cyathostoma*. A number of these characters is not known in *C. lari* and the present account is intended to make good this deficiency in the female, describe the male and extend our knowledge of the species particularly with regard to intra-specific variation. Another reason behind the need for an adequate account of *C. lari* was the discovery within certain Corvidae, taken in the vicinity of St. Andrews, of cyathostomes which might be conspecific with that of the Black-headed Gull.

II. *Cyathostomes* from *Larus ridibundus* L.

Twenty-two specimens of *Cyathostoma*, comprising 17 females and 5 males, were obtained from the nasal and orbital cavities of the Black-headed Gull, *Larus ridibundus* Linn. The identity of the host, the site within the host, the colour of the worm, its striated cuticle, the general shape of its body and buccal capsule, the nature of the caudal spine and the position of the vulva are all characters which agree with those of Blanchard's original description of *Cyathostoma lari*. The general appearance of the body is robust with a more slender anterior third and the tail-spine of the female is small and pointed, (Pl. 11, fig. 11) while the characters of the red perivisceral fluid in which can be seen the whitish loops of the ovaries and the dark brown, sinuous gut are also those of Blanchard's coloured illustration in Cuvier's *Règne Animal*. It is accordingly assumed that these specimens are indeed *C. lari*.

Female.

External.—Of the 17 females two are small and immature and excluded from this description, although their various dimensions are included in the accompanying table. The remainder vary in length from 9.58 to 22.3 mm. and in greatest breadth from 0.46 to 1.08 mm. giving a breadth to length ratio varying from 1 : 20 to 1 : 16, or 5 to 6.25 per cent of the body-length.

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TABLE I.

Serial No. of specimen	Body			Buccal capsule			Oesophagus		Eggs		Vulva
	Breadth	Length	Breadth as % of length	Diameter	Depth	Depth as % of dia- meter	Length	Length as % of body- length	Length	Breadth	Posi- tion behind mouth as % of body- length
1	16.1	1.01	6.3	0.193	0.141	73	0.891	5.6	0.077	0.047	54.4
2	17.25	1.08	6.3	0.220	0.163	74	0.836	4.8	0.083	0.045	55.16
3	9.58	0.50	5.2	0.117	0.091	78	0.67	7.0	0.111	0.035	55.4
4	9.78	0.46	4.6	0.140	0.108	77	0.64	6.6	No shells		55.4
5	13.15	0.70	5.1	0.132	0.112	86	0.74	5.6	0.082	0.044	57.0
6	19.05	1.07	5.6	0.188	0.152	81	0.86	4.5	0.084	0.044	55.0
7	18.5	0.97	5.2	0.270	0.210	78	0.95	5.1	0.083	0.045	54.6
8	16.88	0.98	5.8	0.207	0.141	68	0.92	5.4	0.088	0.044	55.6
9	10.6	0.77	6.0	0.180	0.129	72	0.71	6.7	0.110	0.040	56.4
10	18.75	0.96	5.1	0.255	0.180	71	0.87	4.6	No shells		59.4
11	22.3	1.02	4.5	0.282	0.195	69	1.01	4.5	0.082	0.044	55.2
12	18.0	0.87	4.8	0.240	0.177	74	0.84	4.6	0.082	0.044	55.6
13	15.45	0.83	5.4	0.210	0.195	93	0.18	5.2	No shells		60.0
14	5.5	0.22	4.0	0.083	0.077	93	0.396	7.2	Juv.		57.5
15	4.26	0.18	4.2	0.053	0.045	106	0.396	9.3	Juv.		54.0
16	18.1	0.81	4.5	0.224	0.180	80	0.946	5.2	0.084	0.044	57.8
17	16.34	0.88	5.4	0.211	0.176	83	0.825	5.4	No shell		57.6

Characters of female Cyathostomes from *Larus ridibundus*. Measurements are in millimetres.

Alimentary canal.—The mouth is surrounded by an inflated cuticular ring whose outer margin is indented at six points, Pl. 11, fig. 1. It leads through a reduced aperture, formed by a thin inwardly projecting flange, into a thick-walled, cup-shaped, buccal capsule whose diameter is greater than its depth and whose base is slightly concave on its posterior face. The external diameter of the buccal capsule at its widest point varies from 117 to 282 μ with corresponding depths of 91 and 195 μ : the depth or length of the buccal capsule varying from 71 to 93 per cent of the diameter. A triangular opening in the base of the buccal capsule leads into the oesophagus with a lumen triradiate in section. Surrounding the triangular opening is the armature which in one worm comprises ten teeth, Pl. 11, fig. 2. Three of the teeth are more conspicuous than the others and lie close to the triangular opening, each lying near the centre of one of the sides of this triangle, one being dorsal in position and the two others ventro-lateral. The bases of the remaining teeth extend up the lateral wall of the buccal capsule three lying between the pronounced dorsal teeth and the left ventro-lateral and two lying between the two ventro-laterals and the dorsal and right ventro-lateral. In another worm there are eleven teeth, the additional tooth lying between the dorsal and the right ventro-lateral.

The oesophagus is muscular and clavate, widest towards the posterior end: its length varies from 0.64 to 1.01 mm., or 7.0 to 4.5 per cent of the body length, the longer worms having the relatively shorter oesophagus, Pl. 11, fig. 10. An oesophago-intestinal valve lies in the widening, thin-walled anterior end of the intestine. There is neither ventriculus nor intestinal diverticulum. The remainder of the gut is wide, thick-walled and sinuous, terminating close to the posterior end of the body.

Reproductive system.—The margins of the vulva project and the opening is easily identified if seen in profile. It lies a short distance behind the middle region of the body, its distance from the mouth, expressed as a percentage of the body-length, varying from 54.4 to 60.0 per cent, mean value 56.3 ± 1.65 . The two ovaries, long and of a rather uniform, narrow diameter (125 to 140 μ), are convoluted and twisted on themselves and around the gut, particularly in the middle and posterior regions of the body. Each continues insensibly into an oviduct which narrows to a diameter of 55 μ before opening abruptly into the wide internal end of the uterus, which wide region, with a diameter of 670 μ , functions as a receptaculum seminis. The uteri are long and follow a twisted course narrowing gradually to a diameter of 90 μ and opening separately into the small, spherical ovejector which leads directly to the vulva, Pl. 11, fig. 12. The two uteri show the following differences. The anterior uterus receives the oviduct almost on a level with the vulva, and this uterus forms a loop extending as far forward as the beginning of the intestine and the descending limb narrows gradually as it approaches the ovejector. The loop is twisted on itself and entwined with the wide and sinuous gut. The posterior uterus is similar to the anterior except that it forms a loop which lies posteriorly and the terminal, narrowing limb extends anteriorly beyond the vulva to turn back parallel to the corresponding region of the anterior uterus, but to open into the posterior face of the ovejector. The condition of the reproductive system is fundamentally amphidelphous since the major parts of the two uteri lie, one directed anteriorly and the other posteriorly. These details were made out by dissection of one of the specimens, from which Pl. 11, fig. 12 was made for comparison with Blanchard's figure (1849b, Pl. 7, fig. 5).

Eggs.—Apart from the two juvenile forms already referred to, the specimens all contain eggs, although in four individuals the eggs are unfertilized and without shells. In nine of the remaining specimens the eggs are very uniform in size and shape with a length almost twice the diameter. The egg-shell is almost 2 μ in thickness and shows a slight flattening on one side, it is capped at one end by an operculum which has the form of a biconvex lens 4 μ thick which closes an aperture 8 μ in diameter and there is a thickening similar to the operculum at the other end of the shell. Some of the older uterine eggs possess two opercula. In these nine worms the mean lengths range from 77 to 84 μ and the mean diameters from 44 to 47.5 μ . In the two other worms the size is very variable 86 to 126 μ in length and 35 to 46 μ in breadth: and a character noted in these two worms is that in addition to the eggs with shells there is a large number in which the shell is not formed. Newly-laid eggs and old uterine eggs are segmented. It is concluded from these observations that in the absence of sperms egg-shells are not formed, and that fertilization after the eggs have reached the uterus may result in some eggs continuing without shells, some developing abnormal egg-shells and some, presumably the later arrivals in the uterus, being normal. The sizes of the eggs from the nine worms which yielded eggs of a very uniform size are accordingly taken as the normal values of this specific character.

Male.

The 5 males were obtained from birds in which females were also present, and in one case (σ No. 3, ϕ No. 7) a pair was taken *in copula* but they separated on fixation in hot 70 per cent alcohol. There is considerable variation in a number of structural characters.

External.—The male, much smaller and relatively thinner than the female, is about half her length and one-third of her diameter: the length varies from 6.6 to 9.1 mm. and the maximum diameter from 0.26 to 0.38 mm., giving a diameter to length ratio of 1:22 to 1:26. The caudal bursa is conspicuous and transparent with an entire margin and it projects from the rounded tip of the tail like the bowl of a shallow wine-glass, Pl. 11, figs 7, 8, 9. The supporting rays are typically strongly li-form but they show variation from one worm to another, the most variable part being

the median, unpaired, dorsal ray and its accessory branches, (Text-fig. 1). In two specimens the dorsal ray terminates in a slender filament which supports a high conical extension of the mid-dorsal region of the lip of the bursa. In these two worms the accessory branches, extending to the margin of the bursa, lie towards the apex of the ray and are asymmetrically arranged, two on one side and three on the other. In the three other specimens the conical extension of the lip of the bursa is low and is not supported by the dorsal ray. In these the dorsal ray ends in a series of accessory rays varying in form and arrangement but arising close together towards or at the distal end of the ray. In one worm the arrangement is quite symmetrical. In contradistinction to the variation in the dorsal ray, the other rays are much more uniform in shape and arrangement. In general their shape is digitiform but some rays

TABLE II.

Serial No. of specimen	Body			Buccal capsule			Oesophagus		Spicules	
	Length	Breadth	Breadth as % of length	Diameter	Depth	Depth as % of diameter	Length	Length as % of body-length	Left	Right
1	6.6	0.30	4.5	0.067	0.051	90	0.50	7.5	0.345	0.339
2	6.8	0.26	3.4	0.073	0.068	92	0.51	7.5	0.441	0.423
3	7.6	0.31	4.1	0.097	0.088	91	0.59	7.8	0.384	0.390
4	9.1	0.38	4.2	0.093	0.085	91	0.61	6.7	0.497	0.491
5	6.9	0.28	4.1	0.079	0.060	76	0.52	7.5	0.351	0.300

Characters of male Cyathostomes from *Larus ridibundus*, measurements are in millimetres.

show more pronounced swellings along their length giving them an unduloid surface. The externo-dorsal arises from the base of the dorsal ray and does not reach the rim of the bursa. Lying within the thickness of the wall of the bursa the tip of this ray is bent outwards and applied to the outer wall of the bursa on which it forms a swelling. In the lateral system the postero-lateral and medio-lateral rays arise from a common stem of about half the entire length of these rays, they are closely apposed and extend towards the rim of the bursa, while the antero-lateral ray, united with the other laterals only at its base, bends outwards in the same manner as does the externo-dorsal. In the ventral system the latero-ventral and ventro-ventral rays, united for the proximal third of their length, are similar ; they are closely apposed throughout the remainder of their length and extend to the rim of the bursa.

Alimentary canal.—The mouth, buccal capsule, teeth and oesophagus are similar to those of the female. The buccal capsule varies in external diameter from 67 to 97 μ , and in depth or length from 51 to 88 μ giving a ratio of the latter to the former of 76 to 92 per cent, which falls within the limits of the corresponding values seen in the female. The length of the oesophagus varies from 0.50 to 0.61 mm. being 6.7 to 7.8 per cent of the body-length, values which again do not differ significantly from those of the female.

Reproductive system.—There is a single testis which is convoluted and twisted on itself and on its duct and the two are entwined around the gut throughout the body behind the oesophagus. There are two long and slender spicules. They are brown in colour and each has a transparent, transversely-fluted flange along its inner margin, except at the tip where the two converging spicules are joined together.

There is no constancy either in length or in relative proportions of the two spicules. The length varies from the smallest, $300\ \mu$ on the right side of one worm to the largest, $497\ \mu$ on the left side of another. In two worms the left spicule is definitely the longer, while in the remaining three there is only $6\ \mu$ difference, the right spicule being longer in one of them.

Cytology

The uteri and contents of one worm were fixed, using McClintock's (1929) acetic-alcohol, and squash preparations were made after staining with acetic-orcein (La Cour, 1941). The chromosomes are minute but were sufficiently defined

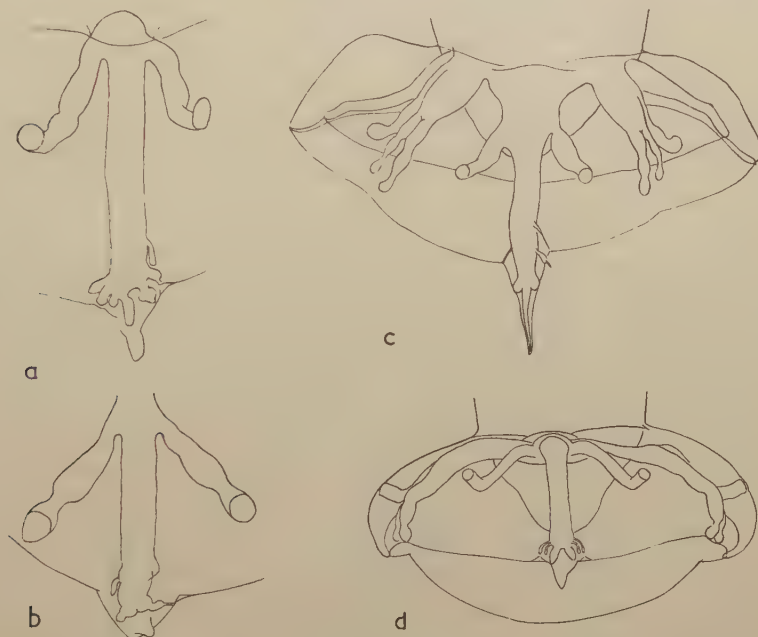


FIG. 1.—*C. lari* from *Larus ridibundus*. a and b—dorsal ray of caudal bursa; c and d—complete caudal bursa.

to make accurate counts. From observations of first and second meiotic divisions of the ovum and mitotic divisions of the zygote it was determined that the female is homogametic with a diploid number of 12 chromosomes and that the male is heterogametic with 11 chromosomes. The worm from which these observations were made agreed in gross anatomical characters with the 17 other females from the same host.

III. *Cyathostomes from Corvidae*.

Throughout the autumn, winter and spring of 1952-53, 60 Corvidae, examined for cyathostomes by one of us, showed the following infestation:

- 26 *Corvus frugilegus* L.—Eight infested with 14 cyathostomes.
- 30 *Corvus corone* L.—Nine infested with 19 cyathostomes.
- 4 *Corvus monedula* L.—One infested with 1 cyathostome.

Amongst these cyathostomes there were but two males, one in *C. frugilegus* and one in *C. corone*. Although the incidence of infestation appears fairly constant in this series,

the number of worms per host is variable. An extreme example of a heavy infestation was seen in a Crow, taken in August 1954, and not included in the above series, in which there were 69 mature cyathostomes including 34 males.

Female.

External.—The general appearance is similar to that of the Black-headed Gull parasite; the living worm is moderately robust and conspicuous by reason of its red colour; also, the brownish gut and white, much convoluted genital ducts and glands can be seen through the transparent cuticle. There is a small terminal spine lying immediately behind the anus and it is curved towards the ventral side. The worms vary in length from 14 to 22 mm. and in width from 0.7 to 1.5 mm. The cuticle in living and freshly preserved specimens is smooth but a fine wrinkling is apparent in some preserved specimens.

Alimentary canal.—The buccal capsule measures 192 to 275 μ in external diameter and 163 to 256 μ in depth, and is armed with teeth varying in number but showing a common pattern in their arrangement similar to that in cyathostomes from the Black-headed Gull, but in the more extensive series examined showing a greater variation.

Three more conspicuous teeth lie, one dorsally and the two others ventro-laterally, each close to the centre of a side of the triangular oesophageal opening. These three teeth are the constant feature of all the worms examined and the arrangement of the remaining teeth is described in relation to these three, Pl. 11, figs 3, 4, 5 and 6. The remaining teeth varying from six to nine lie farther from the oesophageal opening with their bases on the wall of the buccal capsule. Their arrangement is either two teeth between each of the three mentioned above with a total of nine; or two ventrally between the ventro-laterals, and three on each side between the dorsal tooth and the ventro-laterals, with a total of eleven; or two ventrally as before, three between the dorsal tooth and left lateral tooth and two between the dorsal and the right ventro-lateral, giving a total of 10; or 12 teeth in all, three lying between each of the three first described. In the latter case the middle tooth of each group of three is smaller and it lies on the wall of the buccal cavity nearer to the mouth than the teeth on either side of it. The oesophagus is clavate with a length of 6.2 to 4.7 per cent of the body-length, larger worms having a relatively shorter oesophagus. The oesophagus is succeeded by the oesophago-intestinal valve which lies in the anterior, widening region of the intestine. There is neither ventriculus, nor intestinal caecum. The gut is essentially similar to that of the form from the Black-headed Gull.

Reproductive system.—The vulva is similar in appearance and position to that in the form previously described. The proportion of the body-length lying in front of it is 51.3 to 59 per cent (mean 55.5 ± 2.54). The genital apparatus was exposed by dissection and it does not differ from that of the forms in the Black-headed Gull. The condition is amphidelphous, the two uteri entering the spherical ovejector separately and opposite one another and the latter opens directly to the exterior at the vulva. The uterine contents vary, in some uteri eggs are wanting; in others there are ova without shells; in others there are both ova without shells and those complete with shells; and finally in some worms all the eggs possess shells. It is only in the latter case that one gets uniformity in egg-size and egg-shape and it is only such eggs, with egg-shells and opercula fully formed, that are measured to give the character of egg-size. The eggs are prolate spheroids almost twice as long as broad but with one side slightly flattened and with one pole more pointed than the other. In fully formed uterine eggs, that is in those lying close to the ovejector, two opercula are present, one at either pole, although in less developed eggs one operculum alone may be seen. The dimensions of a random sample of 320 eggs from 16 worms are: length 72.6 to 86.2 μ (mean $81.86 \pm 3.44 \mu$) and breadth 39.6 to 48.4 μ (mean $44.1 \pm 1.86 \mu$). The overall dimensions of the egg vary with its development

and accordingly with its position in the uterus. In the beginning of the uterus the egg, irregular in outline and full of refringent granules, becomes, on fertilization, smooth in outline and the shape approximates that of a prolate spheroid. The granules disappear, a thick colourless shell develops, and in this condition the egg is relatively shorter and greater in diameter than the fully formed egg in the terminal part of the uterus, Pl. 11, fig. 13. Measurements of a series of 20 eggs in which the thick shell was apparent was made and compared with those of 20 eggs from the same worm, the latter eggs being fully formed with opercula showing at both poles. There is an alteration in the ratio of length to diameter, and, if one calculates the volume of the egg from the formula for a prolate spheroid $\frac{4}{3} \pi a.b^2$ it is seen that there is an actual diminution in volume as the egg approaches the terminal part of the uterus. The difference between the egg with its newly-formed and thick shell and that when it has assumed its final form is equivalent to a reduction in the thickness of the shell by 2.9μ , assuming the volume of the contained ovum to remain unchanged. As nearly as one can judge, measuring under the microscope, the reduction in thickness of the shell is about 3μ . The actual measurements were: mean of 20 eggs with thick shell $81.56 \mu \times 50.32 \mu$, and mean of 20 eggs with fully-formed shell $85.14 \times 41.8 \mu$.

Male.

External.—The appearance is similar to that of the male worms found in the Black-headed Gull. The caudal bursa is also entire and in some specimens there is a papilla on the mid-dorsal region of its lip which may show a fine filament as in the other forms, Text-fig. 2. The rays supporting the bursa are essentially similar to those already described and they show a similar but more extensive variation in the number and arrangement of the accessory branches of the dorsal ray and in the origin of the externo-dorsals. In some the accessory branches are short and blunt and crowded



FIG. 2.—*C. lari* from *Corvus frugilegus*. Posterior end of ♂ showing caudal bursa and spicules. $\times 75$.

together distally showing a symmetrical arrangement while in others the arrangement is asymmetrical. In some forms the accessory branches are slender and longer, and the lower branches arise about a third of the length of the dorsal ray from its apex, and here also, the arrangement is either symmetrical or asymmetrical. The externo-dorsal rays arising on or near the base of the dorsal ray are seldom symmetrical but always show the character of not extending to the rim of the bursa but being bent outwards within the thickness of the wall of the bursa and applied to its outer face. The rays of the lateral and ventral systems, although varying slightly in thickness, are essentially similar to those of the forms described first in this paper.

Alimentary canal.—The alimentary canal is similar to that of the female. The buccal capsule shows a mean external diameter of 0.098 mm. and a mean length of

0.083 mm. It is armed with teeth similar to, but relatively smaller than, those of the female and their number and the plan of their arrangement is the same.

Reproductive system.—An analysis of the spicule length in 35 specimens shows a variation in length from 350 to 550 μ . The left spicules varying in length from 384 to 550 μ have a mean value of $443.2 \pm 37 \mu$, while the corresponding values of the right spicules are 350 to 499 μ , and $440.4 \pm 28 \mu$. The left spicule is longer in 19 specimens, the right longer in 12, while in four the difference in length is less than 2 μ . It is curious to note that the mean length of the left spicules is very close to that of the right, although the difference in length between the left and right spicule in each worm varies from zero to 66 μ , the mean difference being 17 μ . The common features of the spicules are the brown colour, the united tips and the transversely fluted or fimbriated flange along the inner margin of each spicule.

Cytology

Squash preparations of the contents of uteri were prepared in the same way as those of the parasites of the Black-headed Gull. It was determined that in this case also the diploid number of chromosomes is 12 in the female and 11 in the male. There was not apparent any character of the chromosomes by which the parasites of the Crow could be distinguished from those of the Black-headed Gull.

IV. *Cyathostome from the Redshank.*

A single female cyathostome was taken at St. Andrews from the orbital cavity of a Redshank, *Tringa totanus* (Linn.). It has the appearance of *Cyathostoma lari* and shows the following characters. Length 15.4 mm., maximum breadth 1.12 mm. and ratio of breadth to length of 7.3 per cent. Genital aperture situate 52.8 per cent of body-length behind the mouth. Buccal capsule with maximum breadth of 0.180 mm. and length of 152 mm., and armed with ten teeth arranged as in the previously described forms. Eggs present in the uterus, some with and some without shells; size variable as in other specimens with shell-less eggs, and measurements show a length of 77 to 84 μ and a diameter of 44 to 48 μ . It is of interest that a male was not found, but a male must have been present as there were sperms in the receptaculum seminis.

V. *Cyathostomes from Herring Gull.*

An immature Herring Gull, *Larus cinereus* Brisson, was infested in its nasal and orbital cavities with a dozen female cyathostomes. These showed the following characters.

External.—Length varying from 17.3 to 25.8 mm. with a ratio of maximum breadth to length of 4.5 to 5.1 per cent. Terminal spine as in other female worms. Vulva situate posteriorly to middle of body being 54.0 to 55.6 per cent of body-length behind the mouth the mean value being 54.85 ± 0.24 per cent.

Alimentary canal.—The buccal capsule varies in maximum external diameter from 237 to 308 μ and in depth from 168 to 253 μ giving the depth expressed as a percentage of the diameter of 77 to 86 per cent. The oesophagus varies in length from 0.83 to 1.1 mm. The teeth, variable in size from one worm to another, are arranged on the same plan as in the other worms and those examined show a variation from 10 to 12 in number.

Eggs.—The mean length, and diameter was determined in each worm in which all the uterine eggs had shells and the range of mean lengths in these worms is 85.1 to 87.7 μ long and 43 to 45.5 μ in diameter.

VI. DISCUSSION.

Blanchard's (1849) general description of *Cyathostoma lari* applies in every detail to the appearance and external features of the cyathostome found by us in the Black-headed Gull. The five specimens which he obtained, measuring 10 to 13 mm., are comparable with the smaller specimens obtained by us. It is however in his description of the internal organization that three discrepancies are found, and these are the following. Blanchard describes the wall of the gut as being "mince, très délicat" while we observe the wall to be comparatively thick and robust. With regard to the reproductive system of the female he says "Ces deux tubes ovigères s'élargissent graduellement de manière à former l'un et l'autre un utérus d'une vaste capacité; ils se réunissent pour former un oviduct d'une longueur d'environ 2 millimètres, qui se rétrécit graduellement jusqu'à son orifice." We find in every specimen dissected that the oviduct enlarges abruptly to form the uterus: or, to express it quantitatively, the oviduct measures about $90\ \mu$ in diameter at its point of entry into the uterus, and the rounded beginning of this latter part, which also functions as a receptaculum seminis, measures about $420\ \mu$ in diameter. The other difference is equally significant and concerns the description of the union of the two uteri to form an oviduct 2 mm. in length. The amphidelphous condition where the two uteri open separately into the ovejector which in turn opens directly to the exterior at the vulva is constant in all the forms examined. One might also mention the intestinal diverticulum shown in his figure (*Règne Animal*, pl. 23, fig. 6a) which is not referred to in the text. A diverticulum is wanting in all our specimens, but as it is also absent from the gut of the sclerostome of the horse which Blanchard says the gut of his species resembles, we will not consider this further.

The first point to consider is whether our form from the Black-headed Gull and Blanchard's are different or the same species. The evidence for the former view rests on the first three anatomical differences just mentioned. The view that they are the same species, however, is supported by the general appearance and every other anatomical character described by him and one is forced to the conclusion that Blanchard has misinterpreted a few of the structures he has described. Although it is over a hundred years since he described *Cyathostoma lari* from the orbital cavities of the Black-headed Gull, it appears reasonable to assume that this similar strongyli-form worm from the same site of the same host is the same species, and until a cyathostome is found with the identical peculiarities of the gut and female genital tract mentioned by Blanchard our species must be considered as *Cyathostoma lari*.

We accordingly give a re-description of the genus, altered so as not to exclude the genotype *C. lari* on account of hitherto unknown characters of that form, and give also a revised definition of *C. lari*.

Cyathostoma.—Strongylidae. Sexes not permanently joined in copula. Buccal capsule of both sexes large, cup-shaped, with six to twelve teeth arranged around the oesophageal opening, on the base or on the base and basal region of the lateral walls of the capsule. Oesophagus clavate. Excretory pore anterior to oesophago-intestinal junction. Male with typical strongiliform bursa; rays, compared with those of *Syngamus*, relatively slender, and externo-dorsal ray of bursa leaves median dorsal stem almost at its root. Spicules long and slender, an accessory piece may be present. Vulva in the middle third or anterior third of the body.

Genotype *Cyathostoma* Blanchard, 1849.

Owing to the great variation in the measurable or quantitative characters of these cyathostomes the question of the conspecificity of the forms found in different hosts can only be answered by a comparison of the characters of these forms. The female cyathostomes from the Rook, Crow and Jackdaw are indistinguishable: they are

similar in size and bodily proportions, they show the same proportions in the buccal capsule and are similar in the general plan of the arrangement and in the number of the teeth while the fully formed normal eggs show similar variations in size and a statistical comparison shows that they are not significantly different. There is a large population of males known from the Crow, a single male from the Rook but none from the Jackdaw. The single male from the Rook is almost identical with one of the males from the Crow. The corvid cyathostomes are accordingly considered to be one species.

A statistical analysis similar to that made comparing the female worms from Crow, Rook and Jackdaws was made comparing corvid parasites as a whole with parasites from the Black-headed Gull. An analysis of teeth, bodily proportions, relative size of oesophagus, position of vulva and dimensions of eggs showed that there was no significant difference between the females. The males showed great variation in the size and arrangement of the branches of the dorsal ray of their bursa, as in the sizes of the spicules. Each of the five males from the Black-headed Gull shows an arrangement of the branches of the dorsal ray comparable with one or more of the 35 males from the Corvidae. An analysis of spicule size showed that in spite of the great variation in each group of parasites there is no significant difference between them. It is accordingly concluded that the corvid cyathostome is conspecific with *C. lari*.

Similarly a comparison of the parasite from the Redshank and those from the Herring Gull, with *C. lari* involving female worms alone, shows the identity of all these forms. Although the largest worms were those from the Herring Gull yet there are no significant differences in teeth, bodily proportions or egg-size.

A comparison of the female cyathostomes from the different birds is shown in the accompanying Table III.

Cyathostoma lari Blanchard, 1849.

Habitat : The nasal and orbital cavities of *Larus ridibundus* L. (type host), *L. fuscus* L., *L. cinereus* Brisson (syn *L. argentatus* Pontop.), *Corvus corone* L., *C. frugilegus* L., *Corvus monedula* L. and *Tringa totanus* (L.).

Female.—External : mature forms with a length of 10 to 25.8 mm. and maximum breadth 7 to 5 per cent of the body-length : moderately robust with more slender anterior third, posterior third tapering gradually to terminal spine. Vulva situate posteriorly to the middle of the body, lying 51.3 to 60 per cent of the body-length behind the mouth. Buccal cavity : thickwalled, cup-shaped but broader than deep, armed with 9 to 12 teeth situate on floor of buccal cavity or also extending up sides of cup. Oesophagus clavate and in length 7.0 to 4.25 per cent of body-length. Neither ventriculus, nor intestinal caecum present. Uteri amphidelphous opening into ovejector. Eggs : prolate spheroids 72 to 88 μ in length and 39 to 48 μ in diameter, with slight flattening on one side, with two opercula, one at each pole, forming ultimately in eggs containing embryos : eggs operculate and segmented before oviposition. Diploid number of chromosomes 12.

Male.—External : 6 to 10 mm. long and greatest breadth about 4 per cent of the body-length. Body : slender anteriorly, increasing in breadth to middle region, tapering gradually posteriorly to end abruptly in caudal bursa. Caudal bursa with entire margin, projecting directly posteriorly and with digitiform rays : dorsal ray with accessory branches variable in form and arrangement, externo-dorsal and antero-lateral rays not reaching rim but bent outwards and applied to outer face of bursa, postero-lateral and medio-lateral rays apposed throughout their lengths, as also the two rays of the ventral system. Spicules : brown, slender with thin fimbriated flange along inner margin except at tips where united, 300 to 550 μ long (mean $436 \pm 54 \mu$) and equal, subequal or unequal in length. Gubernaculum present 64 to 77 μ long. Buccal capsule muscular with mean external dimensions 82 μ deep

TABLE III.

	<i>Larus ridibundus</i>	<i>Corvidae</i>	<i>Larus cinereus</i>	<i>Tringa totanus</i>
Size—				
Length (in mm.)	9.58–22.3	14.6–22	17.3–25.8	15.4
Breadth (in mm.)	0.46–1.08	0.7–1.5	0.88–1.3	1.12
Buccal capsule—				
External diameter (in μ)	117–282	192–275	237–368	180
External depth (in μ)	91–210	163–256	168–253	152
Oesophagus—				
Length as percentage of body-length	7–4.5	6.2–4.7	4.7–4.25	5.5
Vulva—				
Position as percentage of body-length behind mouth	54.4–60	51.3–59	54–55.6	52.8
Eggs—				
Length (in μ)	77–88	72–86.2	79–88	77–84
Diameter (in μ)	44–47	39–48.4	42–47	44–48

C. lari may accordingly be re-defined to include all these forms.

and 96 μ in diameter. Oesophagus as in female and in length 7.8 to 6.7 per cent of body-length. Diploid number of chromosomes 11.

VII. ACKNOWLEDGMENTS.

The authors acknowledge with thanks their indebtedness to Mr. S. Prudhoe of the British Museum, Natural History, for his help in identifying the first cyathostomes they obtained; to Professor H. G. Callan for his help in obtaining specimens and advice in the cytological aspect of the problem, and to Mrs. J. Duncan of Easter Balrymonth Farm, Mr. John Brown of Stonywynd Farm and Mr. Herbert Whyte of Winchester Farm for numerous specimens.

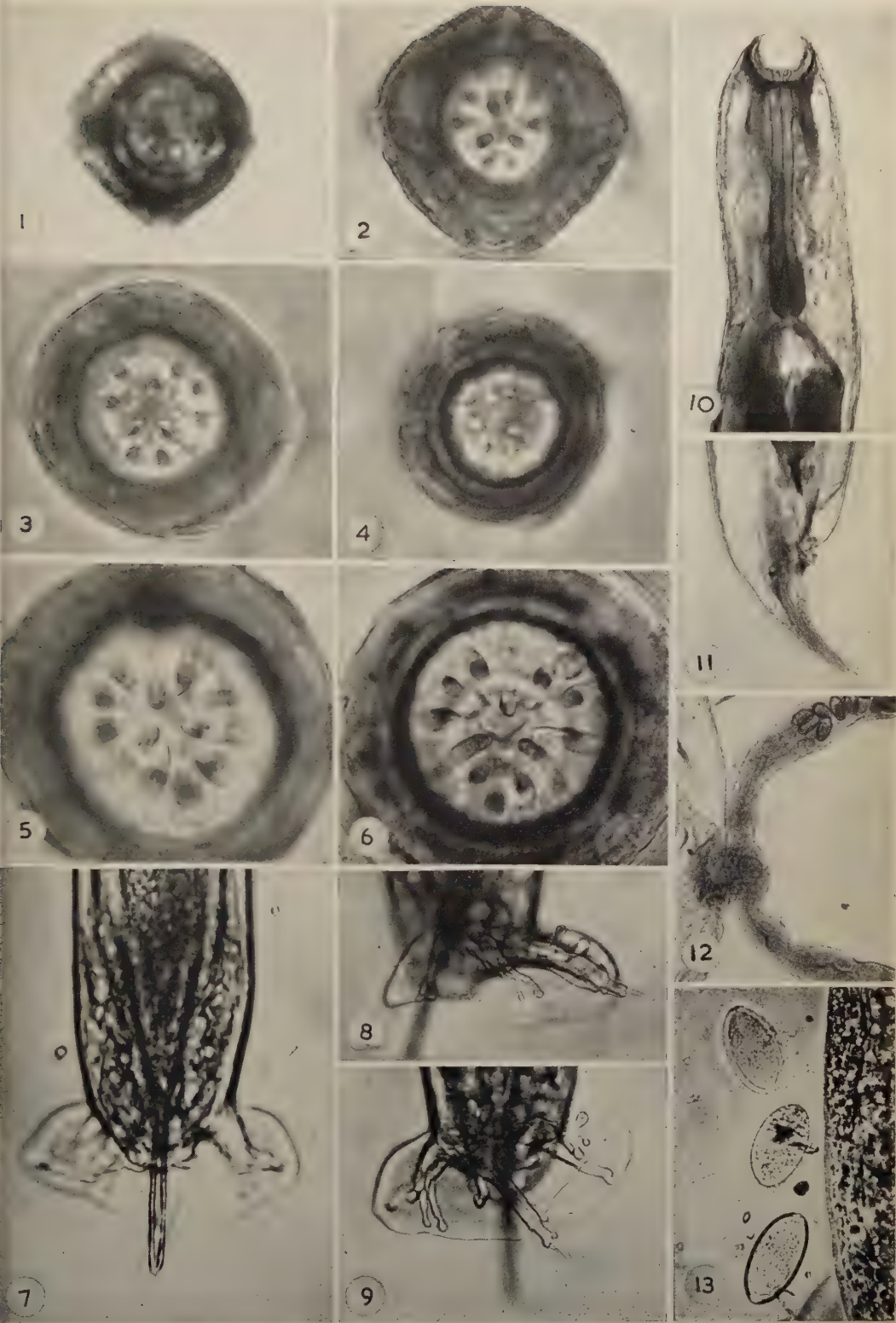
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EXPLANATION OF PLATE II.

Cyathostoma lari E. Blanchard, 1849.

- FIG. 1.—*C. lari* ♀ from *Larus ridibundus*, mouth × 120.
FIG. 2.—*C. lari* ♀ from *L. ridibundus*, buccal capsule with 10 teeth. × 240.
FIG. 3.—*C. lari* ♀ from *Corvus corone*, buccal capsule with 10 teeth. × 240.
FIG. 4.—*C. lari* ♂ from *C. corone*, buccal capsule with 9 teeth. × 240.
FIG. 5.—*C. lari* ♀ from *C. corone*, buccal capsule with 11 teeth. × 240.
FIG. 6.—*C. lari* ♀ from *C. corone*, buccal capsule with 12 teeth. × 240.
FIG. 7.—*C. lari* ♂ from *L. ridibundus*, dorsal view of posterior end with caudal bursa and spicules in focus. × 100.
FIG. 8.—*C. lari* ♂ from *L. ridibundus* caudal bursa in lateral view. × 100.
FIG. 9.—*C. lari* ♂ from *L. ridibundus* caudal bursa in dorsal view with dorsal ray in focus. × 100.
FIG. 10.—*C. lari* ♀ from *L. ridibundus*, anterior end. × 20.
FIG. 11.—*C. lari* ♀ from *L. ridibundus*, posterior end. × 33.
FIG. 12.—*C. lari* ♀ from *L. ridibundus*, ovejector and amphidelphous uteri. × 48.
FIG. 13.—*C. lari* from *C. corone*, uterine eggs showing three stages in the development of the shell. × 178.



Cyathostoma lari E. BLANCHARD.

THYSANOPTERA FROM SOUTH-WEST ARABIA AND ETHIOPIA.

By G. D. MORISON, Ph.D., North of Scotland College of Agriculture, Marischal College, Aberdeen. (Communicated by HUGH SCOTT, Sc.D., F.R.S., F.L.S.)

(With 5 text-figures.)

[Read 24 May 1957.]

I am indebted to the Trustees of the British Museum (Natural History) and to Dr. Hugh Scott for submitting to me for classification two small collections, respectively from South-West Arabia and Ethiopia.

The specimens comprising the former, obtained during the British Museum (Natural History) Expedition to South-West Arabia, 1937-38, were collected in the Western Aden Protectorate in October and November 1937, and in the Yemen in January 1938. They are dealt with here, since the special publication of reports on that Expedition by the Trustees of the British Museum has been discontinued.

The specimens from Ethiopia were collected by Dr. Scott during his two recent journeys, respectively to Southern Ethiopia (Gughé Highlands), 1948-49, and to Northern Ethiopia (high Simien), 1952-53.

Seven species are represented in the collection from South-West Arabia, and six in that from Ethiopia. No species is common to the two collections. Four species are described as new to science, two from South-West Arabia and two from Ethiopia, while a fifth species (*Chiraplothrips* sp., from Ethiopia) may also be new.*

This collection of thirteen species from the mountainous regions of three countries provides a useful basis for the study of the geographical and altitudinal distribution of these species. But the knowledge of the distribution of most species of Thysanoptera is very meagre and there is little to show if any of these species are particularly characteristic of mountain habitats. Further investigation may prove that *Aeolothrips uzeli* and *Taeniothrips meruensis* are more adapted to mountains than the rest.

The insects were preserved in alcohol till I mounted them in Sira mountant in 1954. Their preservation was excellent and they had suffered but little bleaching. The entire collection has been returned to the British Museum. All measurements, length (width) are in $\mu = 0.001$ mm.

TEREBRANTIA.

AEOLOTHRIPIDAE.

Aeolothrips uzeli Bagnall.

Aeolothrips uzeli Bagnall, 1934, *Ann. Mag. nat. Hist.* (10) 13 : 482.

WESTERN ADEN PROTECTORATE : Jebel Jihaf, ca. 7000 ft., 1-19.x.1937, by sweeping, 1 ♀, macropterous (*Scott*).

The insect agrees in so many details with Bagnall's description of the single female (apparently the only specimen yet recorded) in the Vuillet Collection, Paris, from Mongolie-Mandjourie, Ourga à Tsitsihar†, that I consider it should be included under that name despite the 5000-odd miles separating the two localities. Both *Ae. fasciatus* (L.) and *albicinctus* Hal. have a wider geographical distribution in other parts of the world.

* The Thysanoptera collected by the original "Entomological Expedition to Abyssinia", which I conducted jointly with Professor J. Omer-Cooper in 1926-27, were the subject of a paper by Dudley Moulton, 1928, *Ann. Mag. Nat. Hist.* (10) 2 : 227-248. These amounted to 18 species (15 described as new) representing nine genera, but only one of these species is identical with one included in the present paper.—HUGH SCOTT.

† This indicates distribution between Urga in Mongolia and Tsitsihar in Manchuria.

Bagnall's specimen comes nearer in coloration to *Ae. melaleucus* Hal. than *versicolor* Uzel with which he compared it. He did not describe the shape of the head, the sense organs on antennal segments III–IV, the armature on the ventral surface of the second segment of the fore tarsus or the total length of the insect, and the measurements of antennal segments III–V are obviously inaccurate.

The ♀ from Jebel Jihaf is coloured like *Ae. uzeli*, the marginal vein at apex of the fore wing is almost hyaline, scarcely darker than the membrane of the wing in this area. The head ends at the front margin of the eyes, not projecting roundly in front of the eyes as in *Ae. versicolor*. Antennal segment III measures 118 (17), IV 68 (18), V 60 (18), VI–IX 56. Sense organ on III 40 (5), IV 40 (5). Armature is present on the ventral surface of the second segment of the fore tarsus, but owing to the position of the tarsi in the mount, its structure is not clear. Bristles on the posterior margin of abdominal sternite VII are as in *Ae. fasciatus* (L.) Bagnall, that is the two innermost are further apart from one another than each is from the next bristle on its own side. Total length of insect 1624.

THRIPIDAE.

Taeniothrips meruensis (Trybom).

Physopus meruensis Trybom, 1908, Sjoestedt's Kilimandjaro Exped. 16 : 3, pp. 6–7 (figures).

ETHIOPIA : Simien, below the pass of Ras Degien, over 14 000 ft. (highest point reached), 11. xii. 1952, swept from flowering Compositae (probably *Senecio farinaceus* Sch. bip.), 1 ♀, macropterous (Scott).

This species was originally described from Mt. Meru.

The specimen fits Trybom's description, Steinweden's 1933 key, and seems not to belong to any species described from Africa in more recent years.

Taeniothrips debilis Hood.

Taeniothrips debilis Hood, 1925, *Entomologist*, 58 : 136–137.

WESTERN ADEN PROTECTORATE : Jebel Harir, ca. 5000 ft., 3. xi. 1937, beaten from *Jasminum officinale*, 2 ♀, macropterous (Scott).

This species was originally described from Ibadan, Southern Nigeria. Hood's description applies to the two female examples from Jebel Harir.

TUBULIFERA.

PHLAEOTHIRIPIDAE

SMERINTHOTHIRIPS Schmutz.

The generotype of *Smerinthothrips* is *tropicus* which Schmutz described on a ♀ and a ♂. The genus now includes 10–11 described species and some others may yet be transferred to it from other genera. It is closely allied to *Gynaikothrips* in which it was included by Karny in 1921. Within its complex, with rather broadly rounded mouth-cone, fall *Eugynothrips*, *Megeugynothrips*, *Adelphothrips*, *Xiphidiotrips*, *Leptothrips*, *Eothrips*, *Sunaitothrips* and with more sharply pointed mouth-cone *Liothrips*, *Dolichothrips*, and *Adrothrips*, and whilst the generotype of each can be distinguished quite easily, it is not easy to decide the limits of each genus and so where to place some new species which seem not to merit the erection of a new genus. *S. tropicus* is known from Brazil, the other species are recorded respectively from Formosa, Malay States, Singapore, Java, Sumatra, Philippine Isles and India. Six of the species breed in numbers within galls produced by themselves on the leaves of shrubs, trees or creepers. In *Smerinthothrips* I place two apparently new species found by Dr. Scott.

***Smerinthothrips olitorius*, sp. nov. (Fig. 1.)**

Holotype ♀, macropterous: general body colour dark brown with head darker than thorax and abdominal segments I-IV; segments VII-VIII darkest in abdomen; tube dark brown but slightly paler at apex; legs dark brown with fore tarsi and apices of fore tibiae slightly paler than the rest of the fore legs. Antennal segments I dark brown, II yellowish-brown, darkest at base, III-VI brownish-yellow, slightly



FIG. 1.—*Smerinthothrips olitorius*, sp. nov. Holotype ♀; dorsal view of head, antennae, prothorax, fore legs and tube.

darker at apices, VII brownish-yellow shading into dark brown in apical half, VIII dark brown. Fore wings pale brownish-yellow even on base and alula, but with a slightly darker brownish-yellow band from the posterior margin to the bases of the cilia which are brown on fore and hind wings. Hind wings paler brownish-yellow than fore wings. Hairs about the colour of the cuticle from which they arise except three bristles near base of fore wing which are brown and terminal hairs of abdominal segments VIII-X which are brownish-yellow. Subcuticular pigment yellow, sparse.

Measurements: head, length to fore margin of eyes 308 (202, 180), projection of head in front of eyes 20 (78), eye 100 (62), mouth-cone 140 (134), postocular bristle over 48, antennal segments I 39 (39), II 50 (34), III 112 (34), IV 95 (39), V 78 (35),

VI 67 (34), VII 56 (28), VIII 38 (21), total length of antenna 544, pronotum (prothorax plus fore coxae) 128 (380), pronotal bristles, anteromarginal inner and outer 54, midlateral 67, posteromarginal 80, epimeral 94, fore coxal 54, pterothorax 403 (462), fore wing 1180 (average just over 100), three bristles near base of fore wing 76, 81, 86, abdomen 1876 (504), tube 196 (84, 45), longest hairs on tergite IX 175, on tube 190, total length of insect 2808.

Head longer than broad, with vertex overhanging the base of the antennae and slightly raised above the eyes in front. Cheeks are almost parallel, widest between the middle and the base and narrowest at the extreme base. They are but little roughened by transverse striae. Eyes about a third of the length of the head and separated by about the width of an eye and a little shorter on the ventral than on the dorsal surface of the head. They project slightly in front and at the sides and include numerous small facets of which about 15 are seen in optical section of the outer curve. Width across eyes is almost that of head. The pair of postocular bristles is conspicuous. Each bristle is about half the length of an eye and is set at about its own length from the middle of the hind margin of the eye. Mouth-cone broadly rounded. The dorsal outline of the antennal segments is as depicted (Fig. 1) and the segments III–VIII are very slightly more produced ventrally than dorsally. Segment VII slightly constricted at base and with an apex broader than the base of VIII. Pronotum shorter than head. Prothoracic bristles conspicuous, thick, dark, each ending in a hyaline, slightly expanded tip. Legs of moderate length, unarmed. Fore femur only slightly expanded. Fore wing strap-shaped, with smooth, brown cilia and 15–16 duplicated cilia; the three hairs near the base are shaped like those of pronotum. Pterothorax and abdomen of normal shape and chaetotaxy with the long straight hairs of the pterothorax and those of abdominal segments II–VIII tipped like those of pronotum. The long hairs on segment IX are blunt tipped and on X pointed. Tube tapering fairly evenly from base to apex.

The striae on the head behind the eyes are dark, fine, transverse and anastomosing, on the ocellar projection they are reticulate but not conspicuously as in *Gynaikothrips*, fine, anastomosing and chiefly transverse on all legs, pronotum, mesoscutum, abdominal tergites II–IX, longitudinal on metascutum, reticulate longitudinally on abdominal tergite I, absent from tube.

Allotype ♂, macropterous: coloration like that of ♀ but paler brown. On antennal segments III–VII the shading of brown towards the apices is slightly darker. Cuticular striation like that of ♀.

Measurements: head 234 (160–140), projection in front of eyes 20 (68), eyes 90 (47), mouth-cone 112 (100), postocular bristle over 33, antennal segments I 33 (33), II 44 (28), III 84 (28), IV 78 (30), V 67 (28), VI 61 (26), VII 51 (23), VIII 30 (14), total length of antenna 470, pronotum (prothorax plus fore coxae) 90 (262), pronotal bristles, anteromarginal inner 35, outer 40, midlateral 45, posteromarginal 62, epimeral 67, fore coxal 40, pterothorax 278 (303), fore wing 835 (average 72), length of bristles near base of fore wing 43, 46, 49, abdomen 1265 (329), tube 150 (67, 37), long hairs on tergite IX 154, 48, 172, on tube 130–135, total length of insect 1897.

Morphology like that of ♀ except fore wing bears 11 duplicated cilia, the third pair of posterior marginal hairs on tergite IX are stiff bristles 48 long, abdominal sternite IX is produced backwards as a scale 28 long covering the correspondingly deep backward curvature of the anterior ventral margin of the tube. The genitalia are not exposed enough for satisfactory description.

YEMEN: San'a, ca. 7700 ft., 12.i.1938, beaten from foliage, probably wild olive, near vegetable gardens, 8 ♀, 2 ♂ (*Scott*). The ♀ *holotype* and the ♂ *allotype* are mounted on one slide.

Variation in ♀: in coloration, very little; in size: head 313 (218, 190), eye 123 (67), pronotum 117 (336), fore wing 1204 (113), number of duplicated cilia 14–18, length of hairs near base of fore wing 68–76, 81–86, 86–100, prothoracic bristles, anteromarginal inner 50–60, outer 54–67, midlateral 84, posteromarginal 80–95,

epimeral 94-106, tube 207 (88, 44), longest hairs abdominal segment IX 167-190, X 175-200, total length of insect 2630-2934.

Variation in ♂: head 278 (180, 156), eye 100 (50), antennal segment III 102 (30), IV 92 (35), V 75 (30), postocular hair 54, pronotum 112 (303), fore wing 1035 (95), duplicated cilia number 13-14, length of hairs abdominal tergite IX 175, 67, 175, tube size 175 (80, 40), total length of insect 2175.

S. olitorius comes nearest to *citricornis* (Moulton), described under *Gynaikothrips* from Formosa, from which it differs in colour of tarsi, shorter head, antennal segments IV-VI, postocular bristles and tube, and the presence of a pair of well developed inner anterior marginal bristles on the pronotum.

***Smerinthothrips tamariscinus*, sp. nov. (Fig. 2.)**

Holotype ♀, macropterous: body dark brown with head, legs, abdominal segments VII-IX, base of tube, about uniformly dark and darker than thorax and abdominal segments I-V. Tube dark brown, darkest in basal half. Antennal segments I, II dark brown, with II paler yellowish-brown in distal third, III-V yellow with faint brown tinting apices of IV-V, VI yellow shading to pale brown in apical half, VII brown with a yellowish base, VIII brown. Fore and hind wings hyaline with brown cilia. Hairs brown, little darker than the cuticle from which they arise, except that the three hairs near the base of the fore wing are brown and the terminal hairs of abdominal segments VIII-X are brownish-yellow. Subcuticular pigment yellow, sparse.

Measurements: head 353 (202, 190) projection of head in front of eyes 22 (84), eye 117 (56), mouth-cone 140 (134), postocular bristle length about 27, antennal segments I 40 (36), II 54 (32), III 112 (28), IV 90 (30), V 84 (28), VI 67 (28), VII 56 (23), VIII 34 (16), total length of antenna 543, pronotum (prothorax plus fore coxae) 123 (330), length of pronotal bristles, anteromarginal inner 34-45, outer 40, midlateral 60, posteromarginal 67, epimeral 67, fore coxal 40; pterothorax 364 (358), fore wing 1012 (average 95), length of hairs near base 50, 56, 62, abdomen 1543 (506), tube 160 (78, 40), longest hairs on IX-X 156, total length of insect 2630.

Head longer than broad, with vertex overhanging the base of the antennae and slightly raised above the eyes in front. The cheeks are almost parallel, but little roughened by striae. Eyes about a third of the length of the head and separated by about the width of an eye, little shorter on the ventral than on the dorsal surface of the head. Width across eyes is about that of the head. Eyes project slightly in front. Facettes small, numerous, about 15 round the outer curve in optical section of the eye. The pair of postocular bristles is inconspicuous and from examination of 39 other females, each bristle was found to vary in position, length and thickness. The largest bristles found on a female measured 30 and 40 respectively. Each bristle is placed at about one-third to one-half the length of the eye from the middle of the hind margin of the eye. Mouth-cone broadly rounded. The dorsal outline of the antennal segments is depicted (Fig. 2). Segment VII slightly constricted at base and with an apex broader than the base of VIII. Sense cones of moderate length, formula III-1, IV 1-2, V 1-1, VI 1-1, VII 1 dorsal. Pronotum shorter than head, with conspicuous, thick dark bristles each ending in a slightly expanded hyaline tip. Legs of moderate length, unarmed, fore femora scarcely expanded. Fore wing strap-shaped, three hairs near base shaped like those of pronotum, 11-12 accessory cilia, cilia of fore and hind wings smooth. Pterothorax and abdomen of normal shape and chaetotaxy, with the long straight hairs tipped like those of the pronotum except on abdominal segments IX, X on which they are pointed. Tube tapering fairly evenly from base to apex.

Allotype ♂, macropterous: coloration like that of ♀ except that brown shading is darker on apical third of antennal segment V; apical half of VI and VII-VIII are wholly brown.

Measurements : head 340 (180, 173), projection of head 22 (84), eye 117 (50), length of postocular bristles over 20, mouth-cone 123 (118), antennal segments I 40 (32), II 48 (30), III 108 (27), IV 94 (30), V 81 (28), VI 68 (27), VII 57 (22), VIII 32 (16), total length of antenna 526, pronotum (prothorax plus fore coxae) 123 (280), length of prothoracic bristles, anteromarginal inner 46, outer 40, midlateral, postero-marginal 57, epimeral 67, fore coxal 40, pterothorax 330 (354), fore wing 960 (average

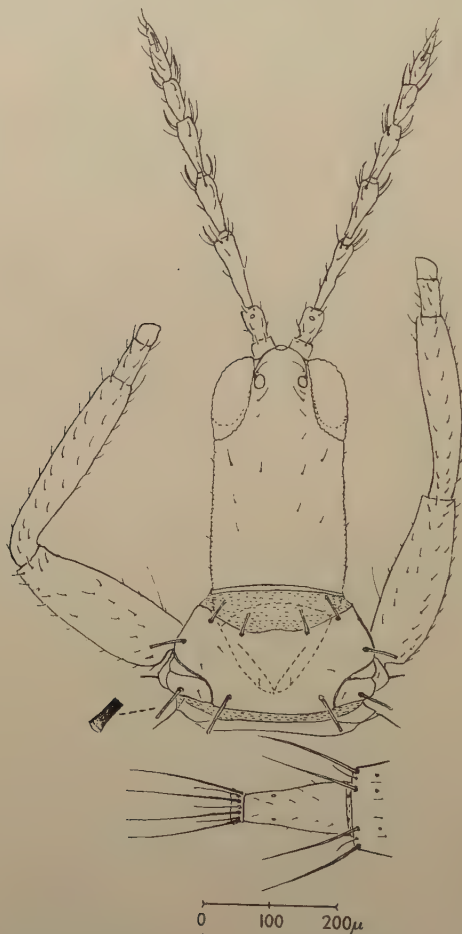


FIG. 2.—*Smerinthothrips tamariscinus*, sp. nov. Holotype ♀; dorsal view of head, antennae, prothorax, fore legs and tube.

84), length of hairs near base of fore wing 46, 57, 60, abdomen 1366 (330), tube 170 (70, 33), length of longest hairs on abdominal segments IX 150, 64, 143, X 135–154, total length of insect 2174.

Morphology like that of ♀, except that postocular bristle in allotype and two other males is usually placed about half the length of an eye behind the middle of the posterior margin of the eye, the fore wing bears 11–12 duplicated cilia, the third pair of posterior marginal hairs on abdominal tergite IX are stiff bristles 64 long, abdominal sternite IX is produced backwards as a scale 30 long covering the corres-

pondingly deep backward curvature of the anterior ventral margin of the tube. The longest hairs on IX are blunt tipped. The genitalia are not exposed enough for satisfactory description. Striae as in *S. olitorius*.

WESTERN ADEN PROTECTORATE: Al Huseini, a few miles north of Lahej, ca. 450 ft., 29.xi.1937, beaten from tamarisk, 40 ♀, 12 ♂ (*Scott and Britton*). The ♀ holotype and the ♂ allotype are mounted on one slide.

One yellow II instar larva taken with the adults may be this species. The holotype bears two eggs inside her body. Each egg is elliptical in outline 350 (196), with a shell ornamented on the outside with polygonal sculpture. Since in 34 out of the other 40 females each specimen bears 1-3 eggs, it seems likely that tamarisk is a larval food plant of this species.

Variation in ♀: in coloration very little, though antennal segments IV-VI may be darker brown towards the apices, as in ♂. Size variation, head 308 (185, 180), 380 (202), antennal segments III 117 (29), IV 100 (29), pronotum 112 (280), fore wing 885 (84), 1190 (106), number of duplicated cilia 6-15 (6-10 on 1 ♀), tube 180 (78, 40), longest hairs on abdominal segment IX 140-170, X 156-178, total length of insect 2000-2830.

Variation in ♂: head 308 (168, 162), postocular bristle 15-30, fore wing 835 (68), number of duplicated cilia 6-12 (6-10 on 1 ♂) tube length 162-180, longest hairs on IX 150-162, X 135-162, total length of insect 2050-2330.

S. tamariscinus is easily separated from *S. olitorius* by its longer head, the shorter postocular and prothoracic bristles and the more slender antennae; amongst described species it comes closest to *citricornis* (Moulton) from which it differs in its dark tarsi, shorter tube, shorter antennal segments IV-V, shorter postocular and prothoracic bristles.

Haplothrips nigricornis (Bagnall).

Anthothrips nigricornis Bagnall, 1910, *Ann. S. Afr. Mus.* 5: 425.

Haplothrips nigricornis Faure, 1955, *Journ. ent. Soc. S. Afr.* 18: 208-218 (figures).

ETHIOPIA: Simien, below the pass of Ras Degien, over 14,000 ft. (highest altitude reached), 11.xii.1952, swept from flowering Compositae (probably *Senecio farinaceus* Sch. bip.), 2 ♀, macropterous (*Scott*).

H. nigricornis was originally described from South Africa. The two female examples from Simien are very close to *H. wouramboulchii*, described by Moulton (1928) from west of Addis Ababa. Moulton did not compare this species with *H. nigricornis*. The chief differences are: postocular bristle 66 compared with 84 long, the prothoracic epimeral bristle is 100, blunt-tipped against 135, pointed, basal bristles of the wing blunt, not pointed.

Haplothrips articulatus Bagnall. (Fig. 3.)

Haplothrips (Trybomiella) articulatus Bagnall, 1926, *Ann. Mag. nat. Hist.* (9) 18: 548-549; 1950, Priesner, *Bull. Soc. Fouad. 1er Ent.* 34: 94 (key).

WESTERN ADEN PROTECTORATE: Jebel Jihaf, ca. 7000 ft., 1-19.x.1937, by sweeping, 1 ♀, macropterous (*Scott*); Jebel Harir, ca. 5000 ft., 3.xi.1937, beaten from *Jasminum officinale*, 7 ♀, 3 ♂, macropterous (*Scott*).

This species was originally described from Morogoro, Tanganyika Territory. The females accord with Bagnall's very brief description and with Priesner's key. A description of the male is appended below, since it seems undescribed though Bagnall mentioned that male examples were included amongst the specimens he examined and Priesner refers in the key to the shape of the pseudovirga of the male.

♂, macropterous (Fig. 3): general colour of the body brown with head, legs and base of tube the darkest. Antennal segments I, II brown, almost as dark as head, III-VI greyish-yellow, VII-VIII pale brown. Fore tarsus and apical half of fore tibia brownish-yellow. Fore wings hyaline with pale brown alula and small area

near the base. Three bristles near base of fore wing and cilia of both pairs of wings brown. Hind wings hyaline. Subcuticular pigment crimson. Older specimens are more homogeneously dark brown and brown pigment may colour the cuticle of antennal segments III–VI, being darkest dorsally and intensifying towards the apical segments.

Measurements: head 180 (168), eye 72 (44), postocular bristle 54, mouth-cone 84 (95), antennal segments I 19 (27), II 32 (27), III 35 (27), IV 50 (30), V 43 (24),

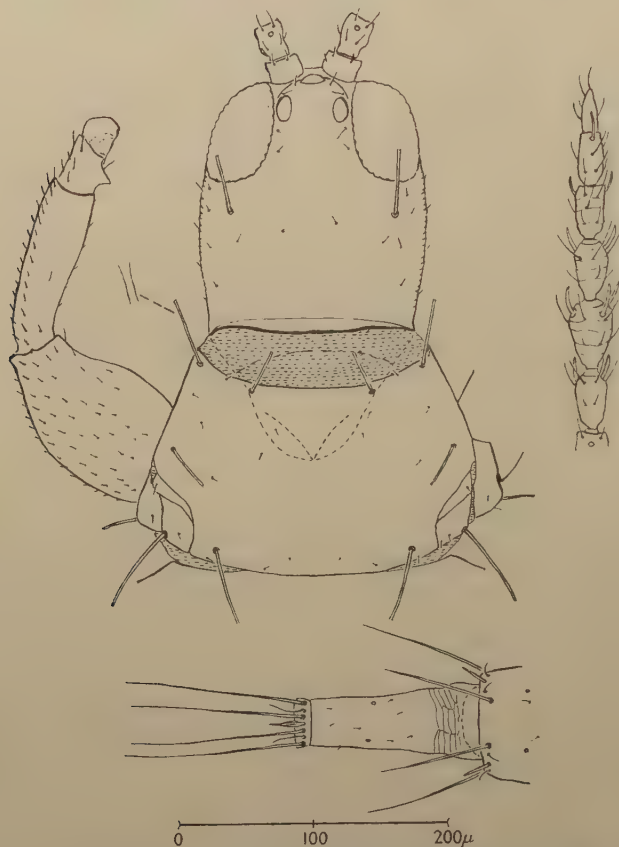


FIG. 3—*Haplothrips articulosus* Bagnall ♂; dorsal view of head, right antenna, prothorax, left foreleg and tube.

VI 40 (22), VII 38 (19), VIII 27 (12), total length of antenna 308, sense cone formula III 1–1, IV 2–2, V 1–1, VI 1–1, pronotum 140 (285), pronotal bristles, anteromarginal inner 32, outer 48, midlateral 32, posteromarginal 60, epimeral 70, fore coxal 32, pterothorax 294 (336), fore wing 784 (108 base, 56 middle, 72 apical widest), length of hairs near base of fore wing 50, 48, 54, abdomen 1060 (308), tube 124 (60, 32), longest hairs on abdominal tergite IX 100, 30, bristle 121, X 135, total length of insect 1695.

The cilia of both wings are smooth, the pseudovirga is tongs-shaped at the apex as stated by Priesner. The tube is encircled near its base in both sexes by white reticulate striation, as indicated in Fig. 3.

Haplothrips gallarum Priesner.

Haplothrips gallarum Priesner, 1950, *Bull. Soc. Fouad. 1er Ent.*, **34** : 80.

WESTERN ADEN PROTECTORATE : Jebel Harir, ca. 5000 ft., 3.xi.1937, beaten from *Jasminum officinale* (together with the specimens of *H. articulatus* recorded above), 1 ♀, macropterous (*Scott*).

Priesner described this species from Morocco.

Haplothrips tolerabilis Priesner.

Haplothrips tolerabilis Priesner, 1936, *Bull. Soc. Roy. Egypte*, **20** : 96.

WESTERN ADEN PROTECTORATE : Jebel Harir, ca. 5000 ft., 3.xi.1937, beaten from *Jasminum officinale* (together with the specimens of *H. articulatus* and *H. gallarum* recorded above), 1 ♂, macropterous (*Scott*).

Priesner has recorded this species from Libya, the Sudan, the Hejaz and the Yemen.

[?] Chiraplothrips sp.

A single micropterous female specimen may be referable to this genus, but is too damaged to be reliably named. It lacks ocelli and sigmoid bristles on abdominal tergites II–VII, but has the areola nearer the base than the apex of antennal segment II ; one sense cone on III, two on IV and an outwardly curved hook on the fore femur.

ETHIOPIA : Simien, below the pass of Ras Degien, over 14,000 ft. (highest point reached), 11.xii.1952, swept from flowering Compositae (probably *Senecio farinaceus* Sch. bip.), 1 ♀, micropterous (*Scott*). The specimen was swept from the flowers together with those of *Taeniothrips meruensis* and *Haplothrips nigricornis* recorded above.

Elaphrothrips impensus, sp. nov. (Fig. 4.)

Holotype ♀, macropterous : general body colour very dark brown, legs as dark as body, fore wing very pale yellow, almost hyaline with light brown shading at extreme base, hind wing paler ; cilia pale brown ; antennal segments I, VI–VIII as dark brown as body, II dark brown at base, shading to yellowish-brown in distal half and palest ventrally, III yellow, shaded brown near apex, IV yellow, shaded brown on apical third, V yellow with apical half brown ; all long bristles pale yellow, blunt-tipped ; subcuticular pigment crimson.

Measurements : head length to fore margin of eyes 515, width across eyes 262, narrowest behind eyes 218, widest 246, at base 234, projection in front of eyes 50 (140), eyes 123 (72), mouth-cone 196 (168), bristle length, interocellar 140, postocular first 224, second, over 100, anterior spine of cheek 48, antennal segments I 56 (52), II 72 (46), III 207 (45), IV 180 (50), V 156 (44), VI 100 (33), VII 84 (28), VIII 75 (22), total length of antenna 968, pronotum 234 (560), prothoracic bristles length, anteromarginal inner 75, outer 86, midlateral 86, posteromarginal 135, epimeral 190, fore coxal 100, pterothorax 506 (608), fore wing 1770 (163 average), its bristles length about 84, 112, 168, abdomen 3364 (740), tube 504 (150, 67), longest hairs on abdominal tergite IX 600, 620, X 450, total length of insect 4655.

Striae normal in distribution, those on the sides of the head giving a slightly uneven outline to the cheeks. Dorsal outline of head is shown in Fig. 4. Anterior ocellus a little closer to the posterior pair than they are to one another. It is placed on a small elevation close behind the base of the antennae, and the space between it and the posterior ocelli is somewhat flattened. Eyes separated by about the width of an eye and each occupying about equal areas above and below the head. Facettes numerous, small. The dorsal outline of antennal segments is shown in Fig. 4. Segments III–VIII very slightly more produced ventrally than dorsally ; VI, VII, VIII clearly separated. Sense cones of moderate length ; formula III 1–1, IV

2-2, V 1-1, VI 1-1. Mouth-cone rounded at apex. Legs of moderate length. On ventral surface of fore tibia a row of five bristles, each on a small tubercle. Ventral surface of first segment of fore tarsus with a blunt tooth measuring about half the lateral width of the tarsus. Fore and hind wings, each of about uniform width.



FIG. 4.—*Elaphrothrips impensus*, sp. nov. Holotype ♀: dorsal view of head, prothorax, right fore leg, left antenna and tube.

cilia smooth; fore wing bears 38 duplicated cilia. Pterothorax and abdomen of normal structure and chaetotaxy. Tube tapering fairly evenly from base to apex.

SOUTHERN ETHIOPIA: Walamo Province, Sōddu, ca. 6800 ft., 15.ix.1948, 1 ♀ holotype), macropterous (Scott).

Elaphrothrips includes 130 described species which are distributed in N. and S. America, Asia, Africa, Australasia and perhaps Australia. Many species have been

found amongst dead leaves and they probably feed upon the spores of minute fungi growing on decaying vegetation. *E. impensus* is close to the South African *brachyurus* Bagnall from which it differs in the shorter head, longer antennal segments III-V, and tube; from the East African *nigripes* Jacot Guillarmod in the much smaller head, less spiny cheeks, longer interocular, postocular and pronotal bristles; from the Ceylon *procer* (Schmutz) Priesner in the little shorter head, smaller number of cheek spines, shorter pronotum, coxal bristles and tube.

Macrophthalthrips scotti, sp. nov. (Fig. 5.)

Holotype ♀, macropterous, ovigerous. Head, body and legs uniform dark brown with much crimson subcuticular pigment; wings hyaline, with brown cilia; antennal segments I dark brown, II-VI yellow with brown shading II at base, V in apical third and VI in apical half; VII-VIII brown. Hairs the colour of the cuticle at their bases, usually dark brown.

Measurements: head 386 (230 across eyes, 190 behind eyes, 173 at base), projection of head in front of eyes 40 (78), eye dorsally 123 (72), ventrally, length 200 with minimum separation between eyes 28, postocular bristles, first pair over 108,

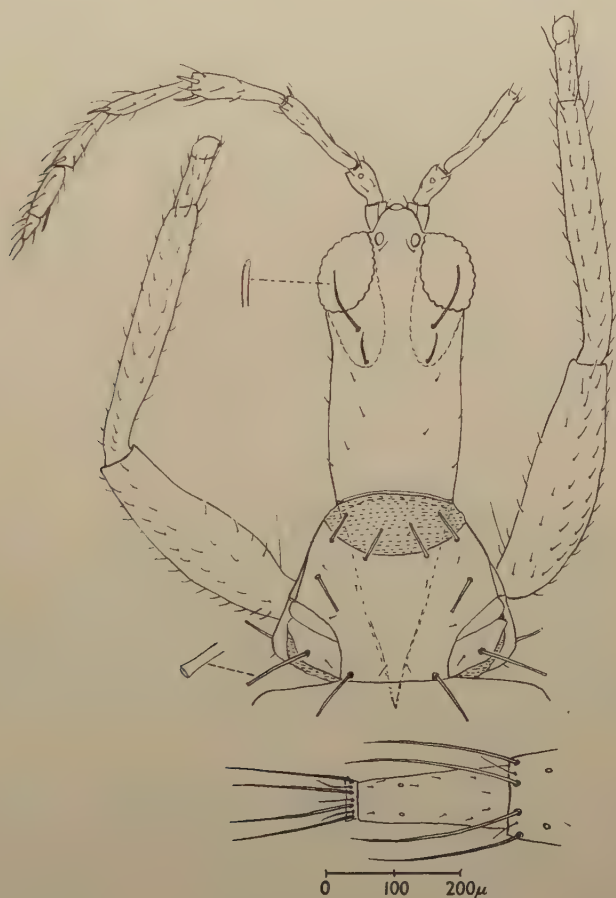


FIG. 5.—*Macrophthalthrips scotti*, sp. nov. Holotype ♀: dorsal view of head, left antenna, prothorax, fore legs and tube.

second pair over 46, mouth-cone 336 (168), antennal segments I 40 (40), II 67 (38), III over 148 (30), IV 143 (35), V 135 (27), VI 108 (27), VII 81 (27), VIII 40 (16), total length of antenna 740 ; pronotum 184 (347), prothoracic bristles, anteromarginal inner and outer, each over 48, midlateral 60, posteromarginal 90, epimeral 108, fore coxal over 40 ; pterothorax 380 (430), fore wing 1500 (95 apical half), tube 230 (94, 56), abdomen 2520 (455), longest hairs on abdominal tergites II 113, IV 154, IX 230-270, X 175, total length of insect 2934.

The dark striae on the head, body and legs are very narrow. The head is almost smooth in outline, without a break between the dorsal and lateral striation. Ocular facettes number about 12 in optical section along the external curve of the eye. The long, pointed mouth-cone reaches the mesosternum. Antennal sense cones rather short and stout, formula III 1, IV 2-2, V 2-1, VI 1-1, VII 1 dorsal, VIII 1 dorsal ; VIII is clearly separate from VII. Pterothorax normal in structure, striae of mesonotum chiefly transverse with few anastomoses, on metanotum chiefly longitudinal with few anastomoses. Legs rather long. Fore legs unarmed. The wings were stuck together and could not be properly separated in the mountant. They are of normal structure with no accessory cilia. Three hairs near the base of the fore wing are hyaline, slightly expanded at the tips, and measure 108, 115, 120. Abdomen of normal shape. The long bristles of abdominal segments II-VIII are dark brown and end like those of the pronotum in a slightly expanded, hyaline tip, on IX, X they taper to points. The sides of the tube are practically straight.

SOUTHERN ETHIOPIA : Walāmo Province, Söddu, *ca.* 6800 ft., 15.xi.1948, 1 ♀ (*holotype*), macropterous (*Scott*).

I have much pleasure in naming the species after Dr. Hugh Scott, F.R.S. who has added so greatly to our knowledge of insects and other organisms from the mountains of distant lands. *M. scotti* is easily separated from the other 15 species of the genus by its dull coloration, the comparatively small degree of projection of the head over the bases of the antennae, the rather wide separation of the eyes, the well developed post-ocular bristles and the rather short mouth-cone. The specimen looks as if it would run rapidly and be capable of jumping, as Hood described in the case of *M. narcissus*. I suspect that the dull coloration is natural and not due to the long soaking in alcohol. The only species described from Africa is the Tanganyikan *M. pulchellus* Hood, which is brightly coloured and conforms more exactly with the genotype, *M. argus* Karny. In coloration and shape of eyes *M. scotti* approaches the East African *Ophthalmothrips pomeroyi* Hood, which has a short, rounded mouth-cone.

***Liothrips nigripes* Moulton.**

Liothrips nigripes Moulton, 1928, *Ann. Mag. Nat. Hist.* (10) 2 : 233.

ETHIOPIA : Simien, Worqa, on west side of Mai Shaha valley, *ca.* 9400 ft., 16.xii.1952, on juniper and/or wild olive, 3 ♀ macropterous (*Scott*).

The original description was based on a single female specimen from Jem-Jem Forest (west of Addis Ababa), between 8000 and 9000 ft., 21.ix.1926 (*Scott*). The three specimens from Simien are very close to *L. laingi* Moulton, described (*op. cit.* p. 232) from a series of specimens also collected in Jem-Jem Forest. In some, probably variable, characters the Simien specimens are intermediate between the two.

IMMATURE AND ADULT STAGES OF SOME BRITISH PHYTOSEIIDAE
BERL., 1916 [ACARINA].* By D. A. CHANT,† Entomology Laboratory,
Belleville, Canada. (Communicated by Dr. F. R. Tubbs, F.L.S.).

(With 26 Text figures.)
[Read 7 November 1957.]

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INTRODUCTION.

For 50 years mites of the family Phytoseiidae have been recognized as predators of phytophagous, orchard-inhabiting mites and considerable interest has been focused on the possibility of utilizing them for the control of pest species. However, our knowledge of the life-histories and habits of these mites is still slight because of the tendency to accept their alleged beneficial qualities without attempting to obtain an understanding of other facets of their lives.

During the years 1952-55 the author studied the ecology of these predaceous mites in south-eastern England, the results of which are to be published elsewhere. Much of this work involved sampling populations in the field at frequent intervals, and it quickly became evident when studying mixed populations that it was insufficient merely to identify and record adult stages, as it was impossible to ascertain whether these fluctuations resulted from invasion or from development unless the abundance of the immature stages had been recorded. The latter could not be done until specific determinations were possible, the immature stages of the species commonly encountered in the study area not having been described or figured previously.

Another reason for undertaking this descriptive work was of broader importance. Evans (1953) stated that the work of Trägårdh had established the major divisions of the suborder Mesostigmata (to which the Phytoseiidae belong), but present knowledge

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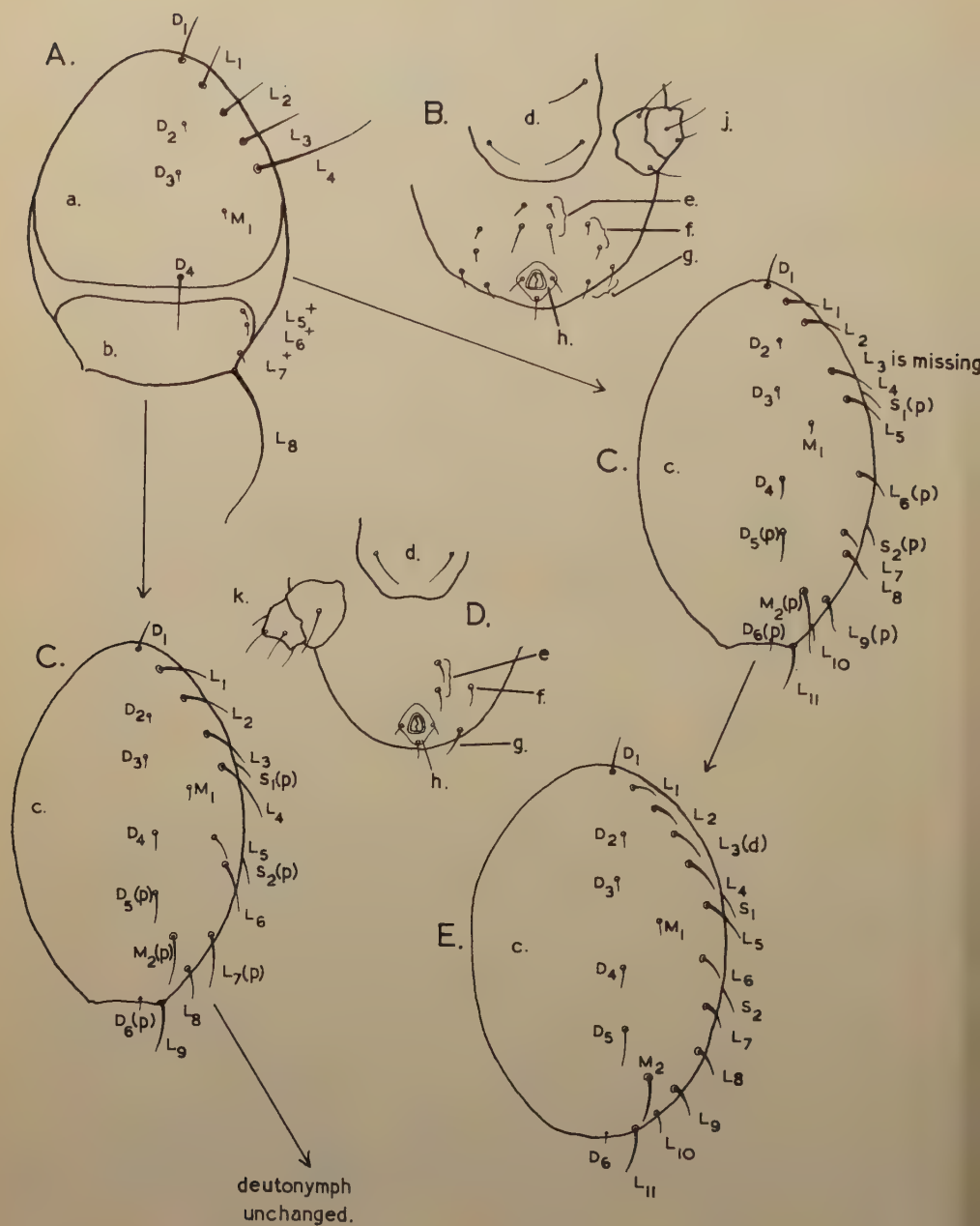


FIG. 1.—Diagram of the two types of setal development in the family Phytoseiidae. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; L 1-11, lateral setae; D 1-6, dorsal setae; M 1-2, median setae; S 1-2, sacral setae; a, anterior dorsal shield of larva; b, posterior dorsal shield of larva; c, dorsal shield; d, sternal shield; e, pre-anal setae; f, lateroventral setae; g, posteroventral setae; h, anal plate; j, coxa and trochanter of posterior larval leg; k, coxa and trochanter of leg IV, protonymph. Setae marked "p" appear during the protonymph, those marked "d" during the deutonymph.

of familial and generic divisions is unsatisfactory and the systems of nomenclature are artificial. He expressed the hope that investigations of the developmental stages of these mites would result in a more natural classification.

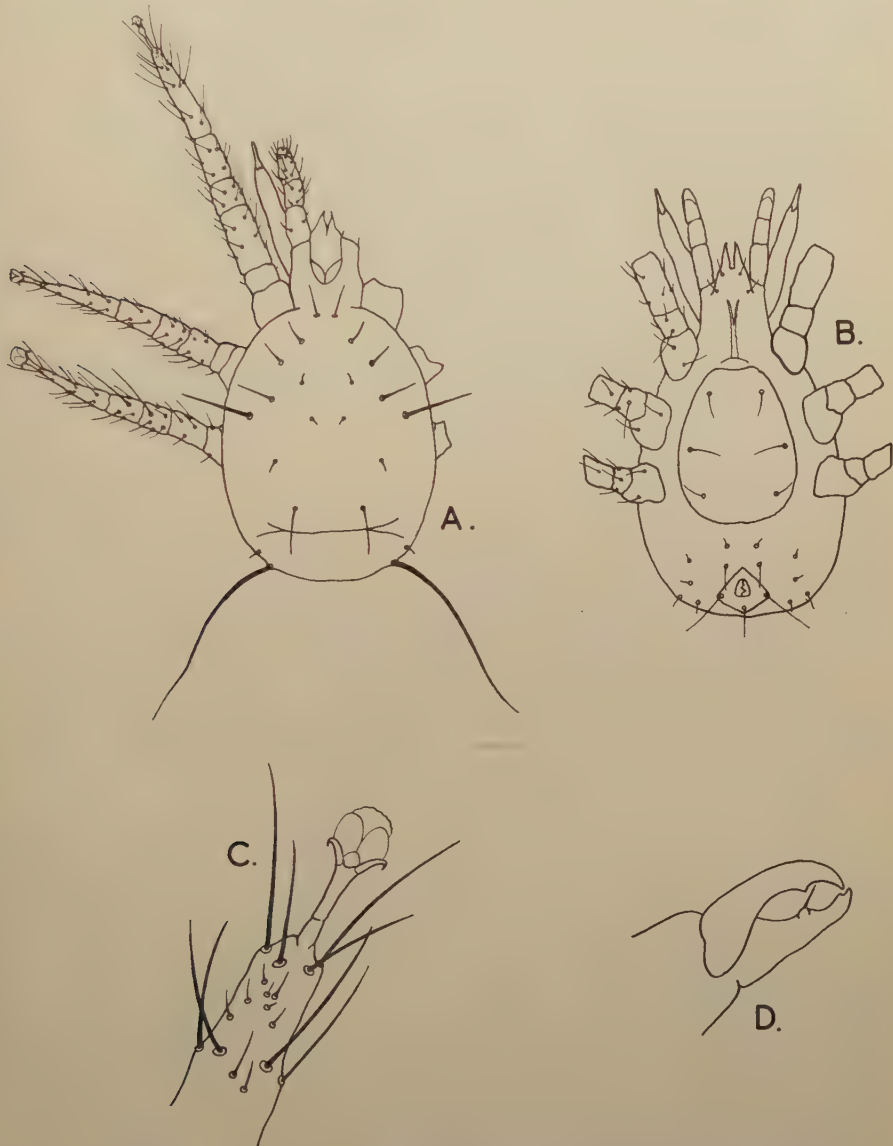


FIG. 2.—*Typhlodromus bakeri* larva. A, dorsal; B, ventral; C, tarsus I; D, chelicera.

Chant (1956) listed the species of Phytoseiidae that occur in south-eastern England and showed that four genera are represented: *Typhlodromus* Scheuten, 1857 (13 species); *Phytoseius* Ribaga, 1902 (one species); *Seiulus* Berlese, 1887 (one species); and *Amblyseius* Berlese, 1914 (one species). Nesbitt (1951) partially revised the family and described in detail the synonymies of these names. To date, the immature stages of only two species in the family have been described. Those of *Typhlo-*

dromus cucumeris Oudemans, 1930, were described by MacGill (1939), who considered the species to be new and described it as *T. thripsti* (see Evans, 1952). The derivation and placement of several important setae are not clear from MacGill's figures. However, some of her observations are useful and the immature stages of this species are included in the keys below. *T. cucumeris* occurs occasionally in southern England, but is rarely found on fruit trees. Evans (1953) made an extensive study of the immature stages of *T. newsami* Evans, a species indigenous to Malaya. His species is also included in the keys below.

Nesbitt (1951) devoted much space to summarizing the anatomical features of the Phytoseiidae. Certain of these features must be mentioned here to clarify discussion. Phytoseiids are mostly minute and generalized, with few diagnostic characters. The gnathosoma is typical of most laelaptids and comprises two portions: the distal portion composed of the epistome and the hypostome; and the proximal portion bearing the palps, which is an extension of the body proper. Beneath the hypostome are the maxillary malae, and above these are the chelate chelicerae. In adult females these are simple shears with curved tips but in males the movable digit bears a spermatophoral process used during copulation.

The idiosoma of the adult is covered dorsally by a single shield, but in the larva there may be two or more such shields. The number, positions, and appearance of the setae on this shield are of taxonomic value and are constant for each species. The ventral surface of the body is covered by a series of plates, or shields, and bears the legs and peritremata. In the female the venter is covered by several plates, the sternal shield being the most anterior, followed by a pair of metasternal plates. The genital shield arises behind the genital opening, or vulva; and behind this lies the ventrianal shield, composed of the anal plate with three para-anal setae and of an anterior extension with a varying number of pairs of setae. The shape and chaetotaxy of this shield also are diagnostic at the specific level.

The ventral surface of the male differs from that of the female by being more heavily sclerotized and covered by only two shields: a sternal shield and a large ventrianal one bearing a variable number of setae in addition to the para-anals.

The interscutal membrane between the dorsal and ventral surfaces usually bears two pairs of setae, though in some species only the anterior pair are present. Evans (1954) showed that in the adult male both these pairs of setae usually occur on the edge of the dorsal shield itself rather than on the membrane.

The legs bear few setae of taxonomic significance, though some segments of the posterior pair of legs (IV) may have setae modified, probably for a sensory function.

Three immature stages were observed in all representatives of the subfamily examined: larva, protonymph, and deutonymph. The sexes are indistinguishable in the first two stages, but in the deutonymph they can usually be distinguished. In *T. newsami*, however, the sexes cannot be distinguished until the mites are adult (Evans, personal communication), and Ballard (1954) found that *T. fallacis* males had only two immature stages. In all species examined during the present work males of both nymphal stages were found.

Both Evans and the present author observed that larvae of these mites have two dorsal shields (Fig. 1), and that these fuse at the first moult to form the single shield of the protonymph and later stages. Bernhart (1955) stated that protonymphal phytoseiids also have two dorsal shields but this was not corroborated by the present work. The anterior larval shield always bears nine pairs of setae arranged in a lateral row of four pairs, a dorsal row of four pairs, and a median pair. The lengths of these vary between species and are used here as taxonomic characters. The posterior larval shield bears setae that vary in number and position. A pair of long, whiplike setae, which Evans considers to be equivalent to M2 in the adult, is always present. However, it can be frequently seen, in specimens mounted immediately before they have moulted, that these correspond in position to the ultimate setae of the lateral series of the nymph and that M2 develops anteriorly to this. Therefore, at present,

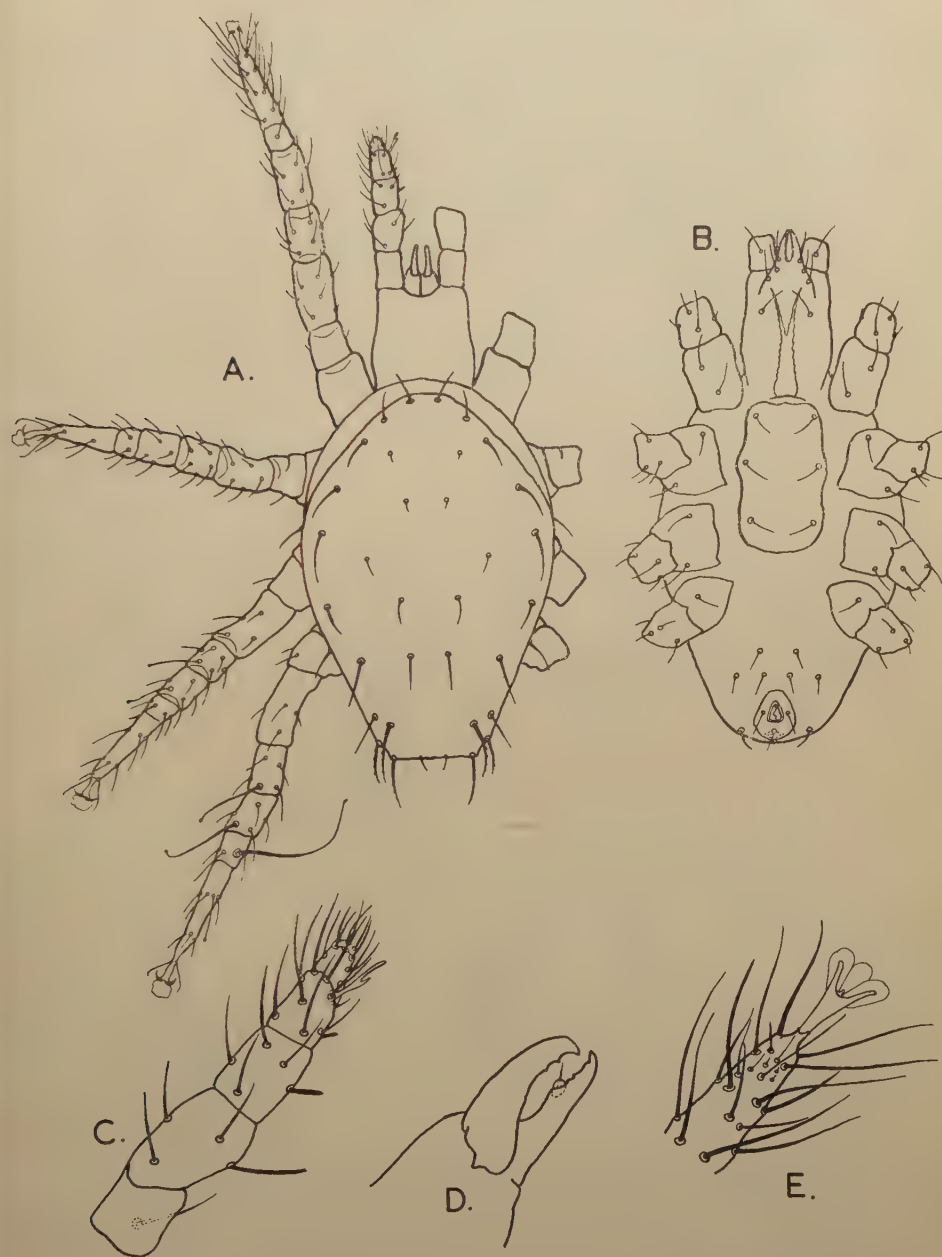


FIG. 3.—*Typhlodromus bakeri* protonymph. A, dorsal; B, ventral; C, pedipalp; D, chelicera; E, tarsus I.

these long setae are considered equivalent to the ultimate setae of the lateral row on the dorsum of nymphs and adults.

Ventrally in the larvae there is a sternal shield that persists unaltered to the second moult. Initially it bears three pairs of setae but this changes to five at the second

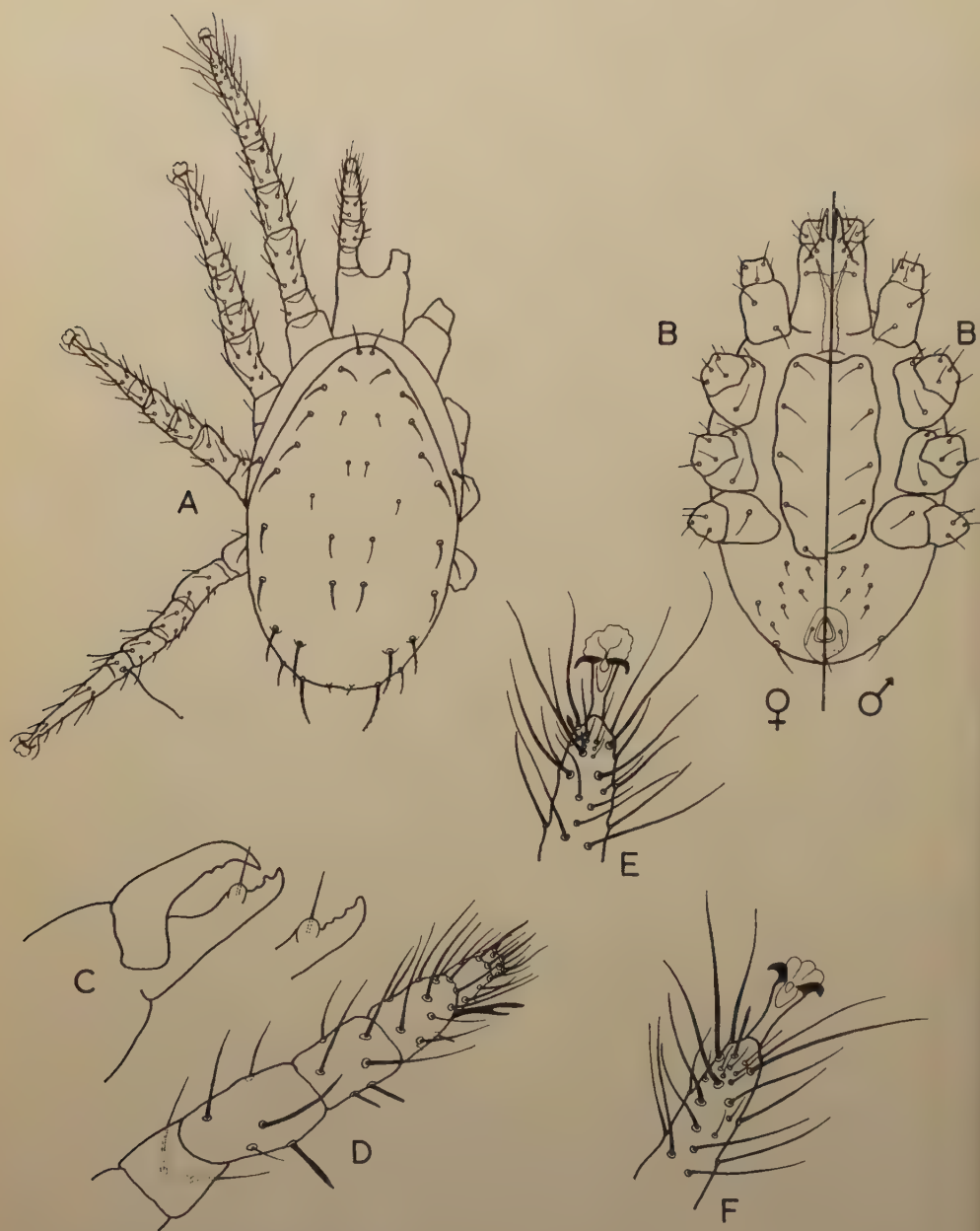


FIG. 4.—*Typhlodromus bakeri* deutonymph. A, dorsal; B, ventral; C, chelicera; D, pedipalp; E, tarsus I, female; F, tarsus I, male.

moult, remaining thus in the adult male. In the female it becomes divided as already described. In all immature stages only a simple anal plate bearing the three para-anal setae is present.

These and other gross features of larval morphology exhibit no differences between species. The hypostome always bears two pairs of setae in the larva, four in the protonymph and later stages. Larval coxae each bear two pairs of setae, which persist throughout development. The fourth pair of coxae is added at the first moult and each of these bears only a single seta.

The setal nomenclature devised by Garman (1948) and discussed by Nesbitt (1951) and Evans (1953) is used throughout this paper. Evans indicated certain disadvantages in this system, the most important being that it disregards development of various setae during the life-cycle of the mites. However, he considered it unwise to introduce a new system until investigations are conducted on allied genera. He also used this system in his description of the immature stages of *T. newsami*, but denoted those setae that appear during the protonymphal stage by the addition of "n1" to the designation and those that appear during the deutonymphal stage by the addition of "n2". In the present paper, in Fig. 1, the letter "p" is added to those setae that appear during the protonymph, and "d" to those of the deutonymph. A more precise nomenclature for the posterior ventral setae of the immature stages is also presented (Fig. 1). This is arbitrary but is useful for descriptive purposes.

All mites described below were reared from females for which specific identifications were available. Mites were mounted on slides in lactic acid, polyvinyl-lactophenol, or de Faure's fluid, and to each was added a small amount of lignin pink stain. Examination was made with a compound microscope, and a projection lens was used in making the drawings. Oil immersion was used for many details of larval chaetotaxy and for the chelicerae of later stages. Whenever possible, measurements of the dorsal shield were taken on 10 specimens of each species, except that in larvae the length from seta D1 to the posterior margin of the posterior dorsal shield was measured.

In all species examined the egg is ovoid and translucent. As the dimensions of the eggs change during development, they are not included below.

***Typhlodromus bakeri* (Garman, 1948).**

Immature Stages.

Larva (Fig. 2): length 201 μ ; width 134 μ ; anterior dorsal shield with nine pairs of setae arranged as normal for the genus. Posterior shield with two pairs of setae on the posterior edge, one long and whip-like, the other minute. Seta D1 slightly longer than L1 or L2; L3 slightly longer than D1. Seta L4 approximately twice as long as L3. Remaining setae minute except for D4, which is only slightly shorter than L4, the longest seta on anterior shield. Ventrally, lateral para-anal setae long and projecting beyond margin of body. Two pairs of pre-anal setae present, the posterior pair long. Beside these, two pairs of lateroventral setae, both minute. Behind these, two pairs posteroventral setae, both minute. In all, six pairs of setae surrounding the anal plate. Movable digit of chelicera with one small tooth, fixed digit with one small tooth and pilus dentilis. Genu and tibia of leg III bearing macrosetae.

Protonymph (Fig. 3): length 234 μ ; width 121 μ ; single dorsal shield with 17 pairs of setae, nine of them in the lateral row. L3 absent. Remaining setae as in adult except compression evident at posterior margin, in that setae M2, L8, L9, and L10 are very close. Lateral setae longer in proportion to body than in adult. Setae S1 and S2 on interscutal membrane. Setae surrounding anal plate reduced to four pairs. Sexes indistinguishable. Movable digit of chelicera with three teeth, the posterior being minute; fixed digit with two teeth and pilus dentilis. Genu and tibia of leg III bearing macrosetae and anterior member of first pair of setae on tarsus also long. Genu, tibia, and basi-tarsus of leg IV bearing long macrosetae with swollen rounded tips.

Deutonymph (Fig. 4): length 272 μ ; width 148 μ ; dorsal shield with 18 pairs of setae, 10 in lateral row, L3 being present. Placement as in adult, though posterior

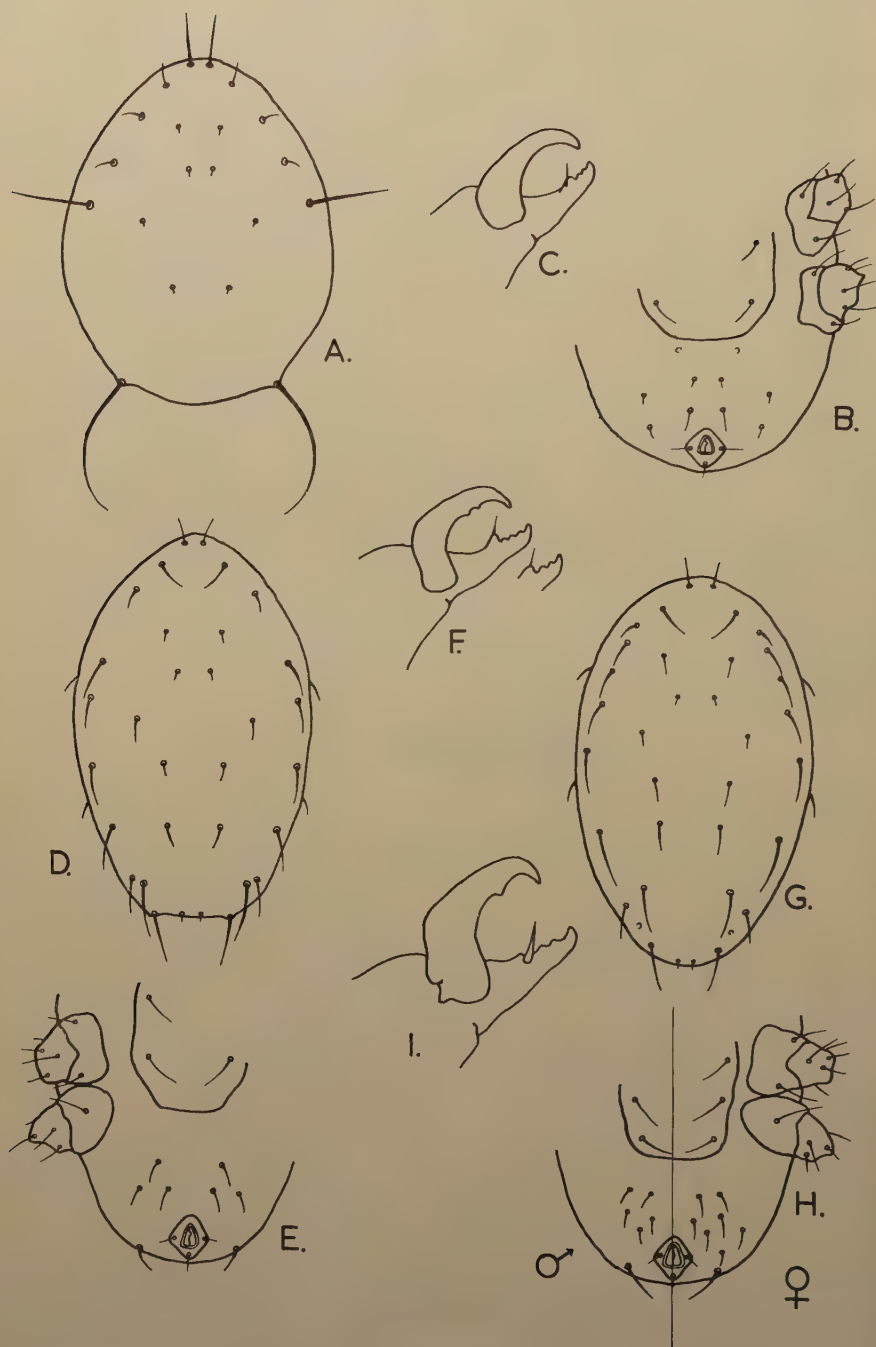


FIG. 5.—*Typhlodromus tiliae*, immature stages. A, larva, dorsal; B, larva, ventral; C, larva chelicera; D, protonymph, dorsal; E, protonymph, ventral; F, protonymph, chelicera; G, deutonymph, dorsal; H, deutonymph, ventral; I, deutonymph, chelicera.

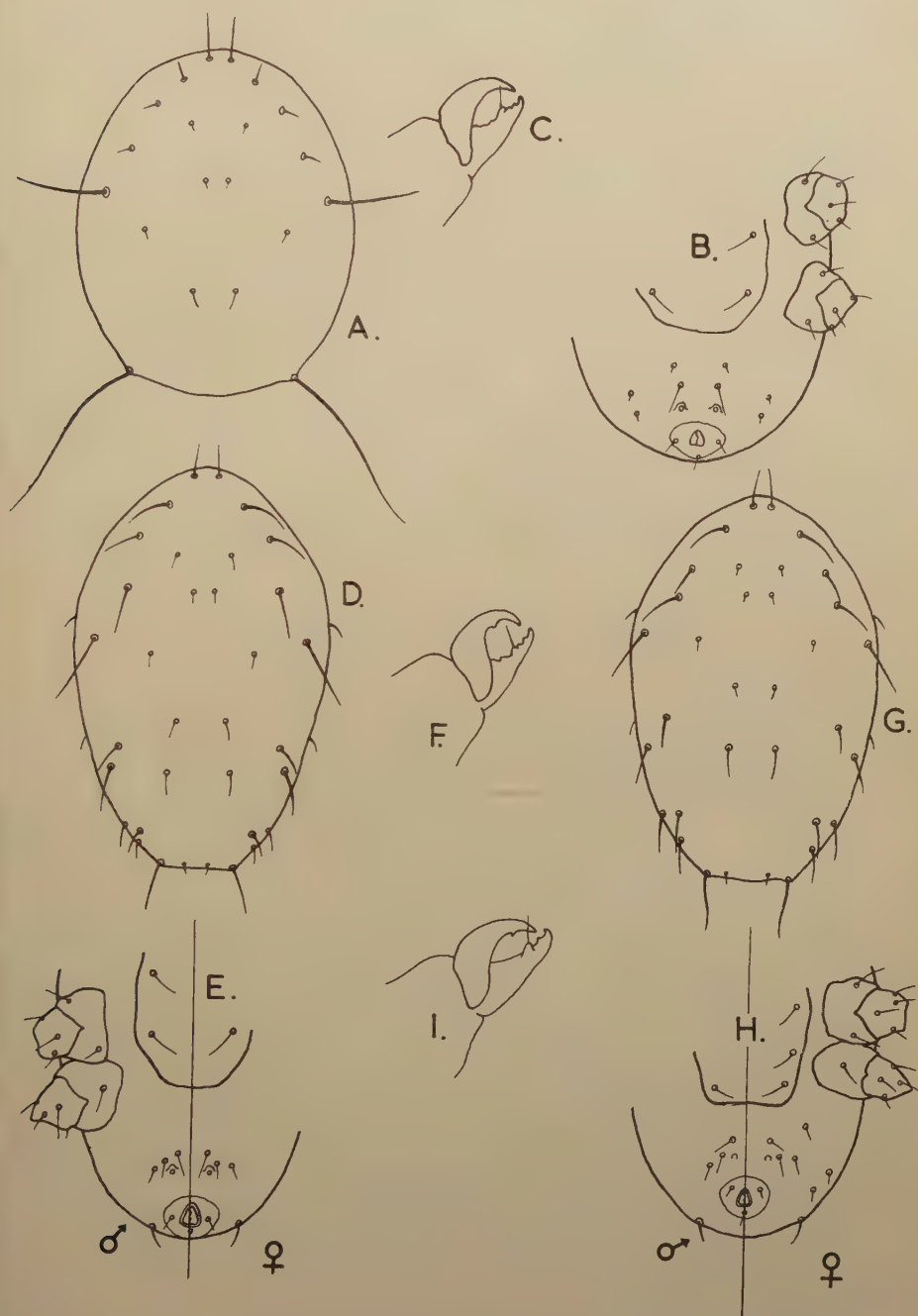


FIG. 6.—*Typhlodromus finlandicus*, immature stages. A, larva, dorsal; B, larva, ventral; C, larva, chelicera; D, protonymph, dorsal; E, protonymph, ventral; F, protonymph chelicera; G, deutonymph, dorsal; H, deutonymph, ventral; I, deutonymph, chelicera.

setae still longer in proportion to body. Setae surrounding anal plate increased to eight pairs in the female nymph, six in the male. Movable digit of chelicera with two or three teeth, the posterior minute when present; fixed digit with two or three teeth and a pilus dentilis. Leg III without macrosetae; those on genu, tibia, and basi-tarsus of leg IV shorter in proportion to leg than in protonymph.

Adult Stages (Figs. 19 and 25).

Female (Fig. 19): length $375\ \mu$; width $208\ \mu$; chaetotaxy of dorsal shield as in deutonymph but setae shorter relative to length of body. Posterior lateral setae and M2 serrated, especially in females of the overwintering generation, where it is accompanied by reticulation of the dorsum. Ventrianal shield present and with four pairs of setae in addition to para-anals. Remaining setae surrounding anal plate of deutonymph situated beside and behind shield. Movable digit of chelicera with two or three teeth; fixed digit with five teeth and pilus dentilis arising adjacent to a ridge that may be a sixth tooth. Macrosetae on leg IV greatly reduced, only that of basi-tarsus being noticeable.

Male (Fig. 25): length $260\ \mu$; width $161\ \mu$; chaetotaxy of dorsal shield similar to that of female except that S1 and S2 are on shield instead of on interscutal membrane. Ventrianal shield present and with five pairs of setae in addition to para-anals. Fixed digit of chelicera with one tooth and pilus dentilis; movable digit with one weak tooth and spermatophoral process.

The adult female of this species was described by Garman (1948), Nesbitt (1951), Cunliffe & Baker (1953), and Womersley (1954). The male was described by Chant (1956).

***Typhlodromus tiliae* Oudemans, 1929.**

Immature Stages (Fig. 5).

Larva: length $165\ \mu$; width $114\ \mu$; anterior dorsal shield with nine pairs of setae arranged as normal in the genus. Posterior shield with one pair of long, whip-like setae. Seta D1 longer than L1, L2, or L3 but much shorter than L4. Dorsal and median setae minute. Two pairs of pre-anal setae present, the posterior pair moderately long. Two pairs of lateroventral setae present, both minute. In some specimens, a pair of pores distinguishable anterior to pre-anal setae. In all, four pairs of setae surrounding anal plate. Movable digit of chelicera without teeth; fixed digit with two teeth and pilus dentilis.

Protonymph: length $227\ \mu$; width $119\ \mu$; single dorsal shield with 16 pairs of setae, eight in lateral row, and L3 absent. Positions of lateral setae as in adult except L8 and L9 relatively closer together and closer to M2, as if posterior margin of shield compressed. Posterior margin of dorsal shield almost square. S1 and S2 on interscutal membrane. Ventrally, four pairs of setae surrounding anal plate. Sexes indistinguishable. Movable digit of chelicera with two teeth; fixed digit with two or three teeth and pilus dentilis. Basi-tarsus of leg IV with macroseta and posterior member of first pair of dorsal setae on tarsus IV also long.

Deutonymph: length $268\ \mu$; width $134\ \mu$; dorsal shield with 17 pairs of setae, nine in the lateral row, L3 present; arrangement as in protonymph but without posterior compression; indistinct pore present between L8 and L9. In female nymph, eight pairs of setae surrounding anal plate, in male only six. Movable digit of chelicera with one or two teeth; fixed digit with two teeth and pilus dentilis.

Adult Stages (Figs 19 and 25).

Female: length $304\ \mu$; width $163\ \mu$; chaetotaxy of dorsum similar to that of deutonymph. Pore between L8 and L9 prominent. Ventrianal shield present and with four pairs of setae in addition to para-anals. Movable digit of chelicera with one or two teeth; fixed digit with two large and one small teeth and pilus dentilis.

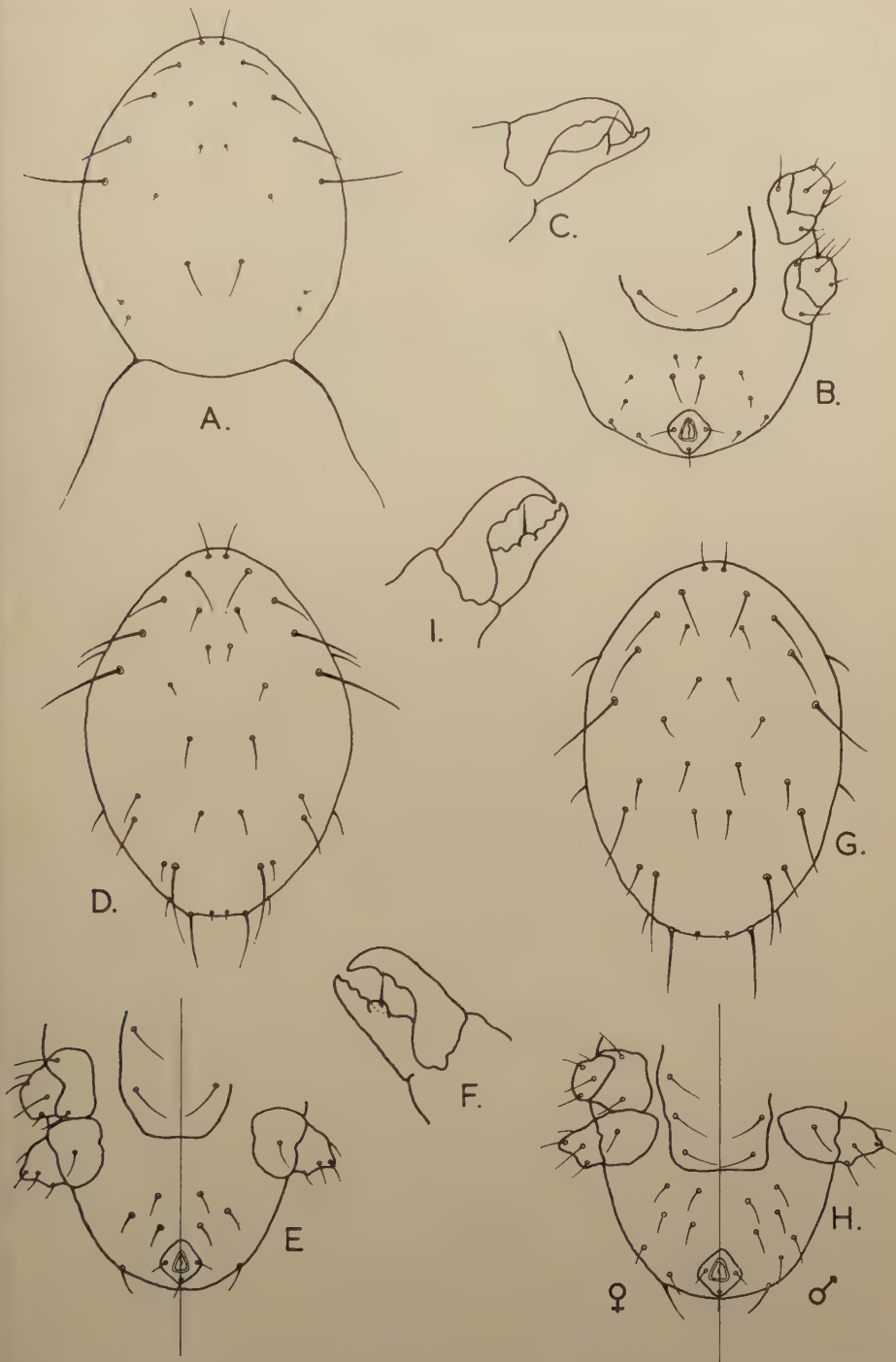


FIG. 7.—*Typhlodromus umbraticus*, immature stages. A, larva, dorsal; B, larva, ventral; C, larva, chelicera; D, protonymph, dorsal; E, protonymph, ventral; F, protonymph, chelicera; G, deutonymph, dorsal; H, deutonymph, ventral; I, deutonymph, chelicera.

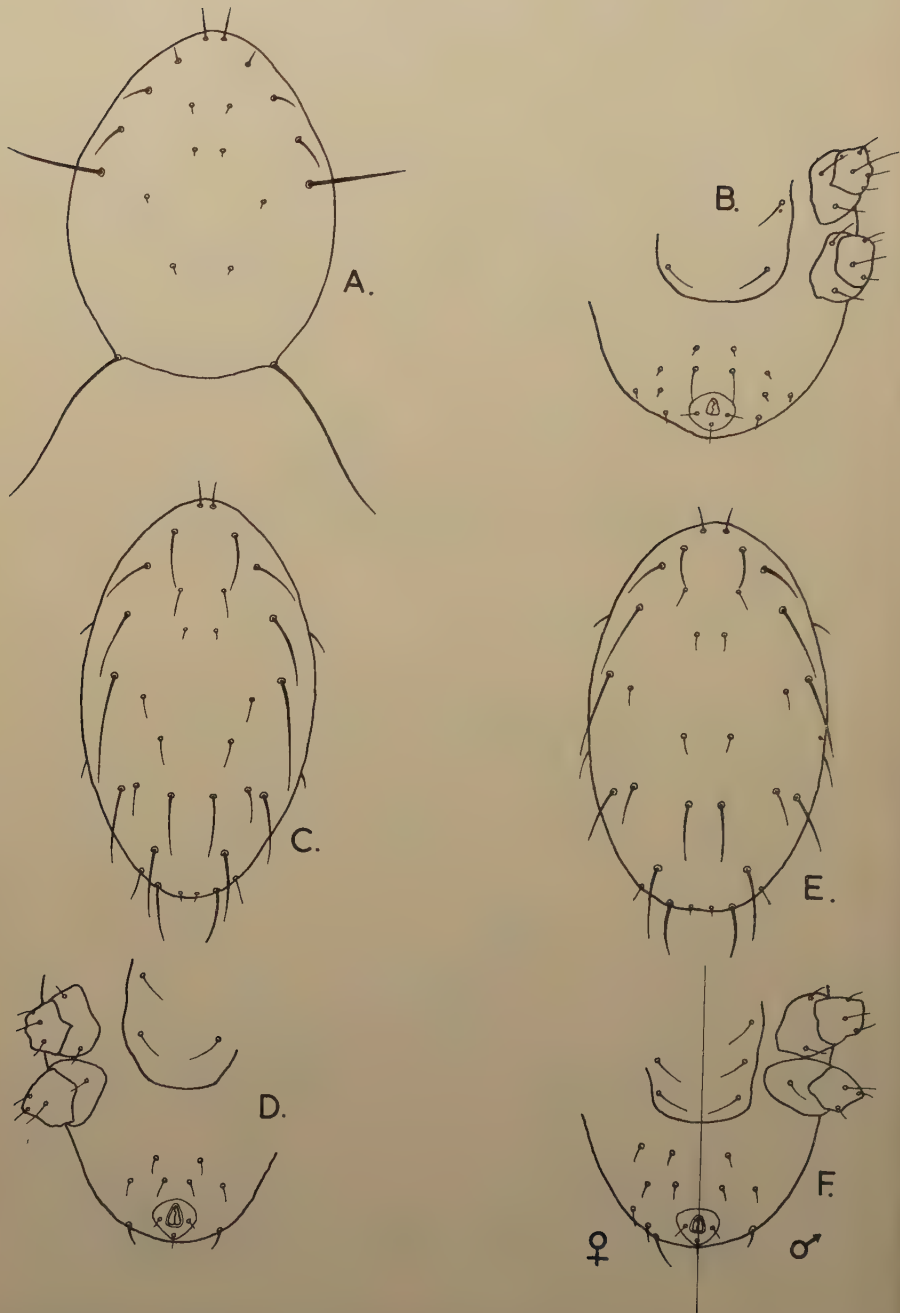


FIG. 8.—*Typhlodromus aberrans*, immature stages, A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

Male: length 234 μ ; width 128 μ ; chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present and with five pairs of setae in addition to para-anals. Movable digit of chelicera with one tooth and horn-like spermatophoral process; fixed digit with one large and one small tooth and pilus dentilis.

The adults of this species were described by Oudemans (1929a), Nesbitt (1951), and Cunliffe & Baker (1953).

***Typhlodromus finlandicus* (Oudemans, 1915).**

Immature Stages (Fig. 6).

Larva: length 198 μ ; width 134 μ ; anterior dorsal shield with nine pairs of setae arranged as normal in the genus. Posterior shield with one pair long, whip-like setae. Seta D1 twice as long as L1, L2, or L3. Seta L4 four times as long as other anterior lateral setae. Remaining setae minute. Ventrally, two pairs of pre-anal setae present, the posterior long and extending to edge of anal plate. Slightly behind these there is a pair of pronounced pores that are characteristic of the species. There are two pairs of lateroventral setae, both minute. In all, four pairs of setae surrounding anal plate. Chaetotaxy of legs distinctive; long setae present on tibia, basi-tarsus, and tarsus of leg I, probably of sensory function. Genu and tibia of leg III with macrosetae thicker than normal, and from three to four times longer. Movable digit of chelicera without teeth; fixed digit with two teeth and pilus dentilis.

Protonymph: length 187 μ ; width 134 μ ; single dorsal shield with 17 pairs of setae, nine in lateral row and L3 present. Setae as in adult except compression evident posteriorly and length of setae longer in proportion to body. Ventrally, four pairs of setae surrounding anal plate. Sexes distinguishable; in male, two pre-anal setae and anterior member of lateroventral setae form a transverse row directed laterad of the posterior margin of the body; in female, posterior member of this row misplaced, appearing laterad rather than lateropostad of the second member. In both sexes a pair of distinct pores associated with pre-anal setae. Setae of tarsus I longer than normal, but shorter in proportion to tarsus than in larva. Macrosetae on genu and tibia III scarcely longer than their companions. Macrosetae on genu, and tibia of leg IV, and a long, thickened macroseta on basi-tarsus IV. Movable digit of chelicera with one tooth; fixed digit with three teeth and pilus dentilis.

Deutonymph: length 287 μ ; width 157 μ ; dorsal shield with 17 pairs of setae arranged as in adult. Setae surrounding anal plate increased to seven pairs in female nymph, remaining at four in male. Arranged as in protonymph. Movable digit of chelicera with one tooth; fixed digit with two teeth and pilus dentilis. Setae of tarsus I normal in length. Leg II without specialized setae. Macrosetae on genu and tibia III, and on genu, tibia, and basi-tarsus IV.

Adult Stages (Figs 20 and 25).

Female: length 335 μ ; width 201 μ ; chaetotaxy of dorsum as in deutonymph. Ventrianal shield present with three pairs of seta in addition to para-anals, and a pair of pronounced pores. Movable digit of chelicera with one tooth; fixed digit with four teeth and pilus dentilis. Genu and tibia III with noticeable macrosetae. Genu, tibia and basi-tarsus IV with strong macrosetae.

Male: length 234 μ ; width 115 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with three pairs of setae in addition to para-anals. The pores are pronounced. Fixed digit of chelicera with two teeth and pilus dentilis; movable digit with two teeth, the posterior being minute, and a spur-shaped spermatophoral process.

The adults of this species were described by Oudemans (1915a and b as *Seiulus*

finlandicus sp. n. ; 1929a as *T. pruni* sp. n. ; 1929b as *T. finlandicus*), Nesbitt (1951) and Cunliffe & Baker (1953).

***Typhlodromus umbraticus* Chant, 1956.**

Immature Stages (Fig. 7).

Larva : length 177 μ ; width 118 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with two pairs of short setae on the anterior margin and one pair of long, whip-like setae on the posterior margin. Seta D1 approximately equal in length to L1 and L2 ; L3 one-third again as long and L4 three times as long as L1 or L2. Remaining setae minute except D4 which is as long or longer than all others on anterior shield except L3 and L4. Two pairs pre-anal setae present, the posterior long. Laterad are two pairs lateroventral setae, both minute. Postad are two pairs posteroventral setae, both minute. In all, six pairs of setae surrounding anal plate. Movable digit of chelicera with two teeth ; fixed digit with two teeth and pilus dentilis. Genu and tibia III with macrosetae.

Protonymph : length 209 μ ; width 130 μ ; single dorsal shield with 17 pairs of setae, nine in lateral row ; L3 present. Compression evident at posterior margin, L8, L9, and M2 being very close together. Setae generally longer in proportion to body than in adult. Setae surrounding anal plate reduced to four pairs in both sexes. Sexes indistinguishable. S1 and S2 on interscutal membrane. Movable digit of chelicera with two teeth ; fixed digit with three teeth and pilus dentilis. Genu and tibia III and genu, tibia, and basi-tarsus IV with macrosetae. Posterior member of the first pair of setae on tarsus IV also long.

Deutonymph : length 225 μ ; width 124 μ ; dorsal shield with 17 pairs of setae, those of posterior margin more widely spaced than in protonymph. Anterior lateral setae longer in proportion to body than in adult. Setae surrounding anal plate increased to seven pairs both in male and female nymph. Sexes indistinguishable. Movable digit of chelicera with two teeth ; fixed digit with three teeth and pilus dentilis. Macrosetae on legs unchanged from protonymph.

Adult Stages (Figs 20 and 25).

Female : length 326 μ ; width 178 μ ; chaetotaxy of dorsum as in deutonymph except setae are shorter in proportion to body. Ventrianal shield present with three pairs of setae in addition to para-anals. A pair of pores present posteromesiad of posterior pair of pre-anal setae. Movable digit of chelicera with two teeth ; fixed digit with three teeth and pilus dentilis. Leg III without specialized setae. Genu, tibia, and basi-tarsus IV with long macrosetae.

Male : length 255 μ ; width 135 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with six pairs of setae in addition to para-anals. Fixed digit of chelicera with seven teeth and pilus dentilis ; movable digit with one tooth and a lobed spermatophoral process.

The adult forms of this species were described by Chant (1956).

***Typhlodromus aberrans* Oudemans, 1930.**

Immature Stages (Fig. 8).

Larva : length 162 μ ; width 105 μ ; anterior dorsal shield with nine pairs of setae arranged as usual to the genus. Posterior shield with one pair of long, whip-like setae. Seta D1 slightly longer than L1 or L2, and equal in length to L3. Seta L4 approximately three times as long as L3. Remaining setae minute. Two pairs of pre-anal setae present, the posterior longer. Laterad are two pairs lateroventral setae, both minute. Postad are two pairs posteroventral setae, both minute. In

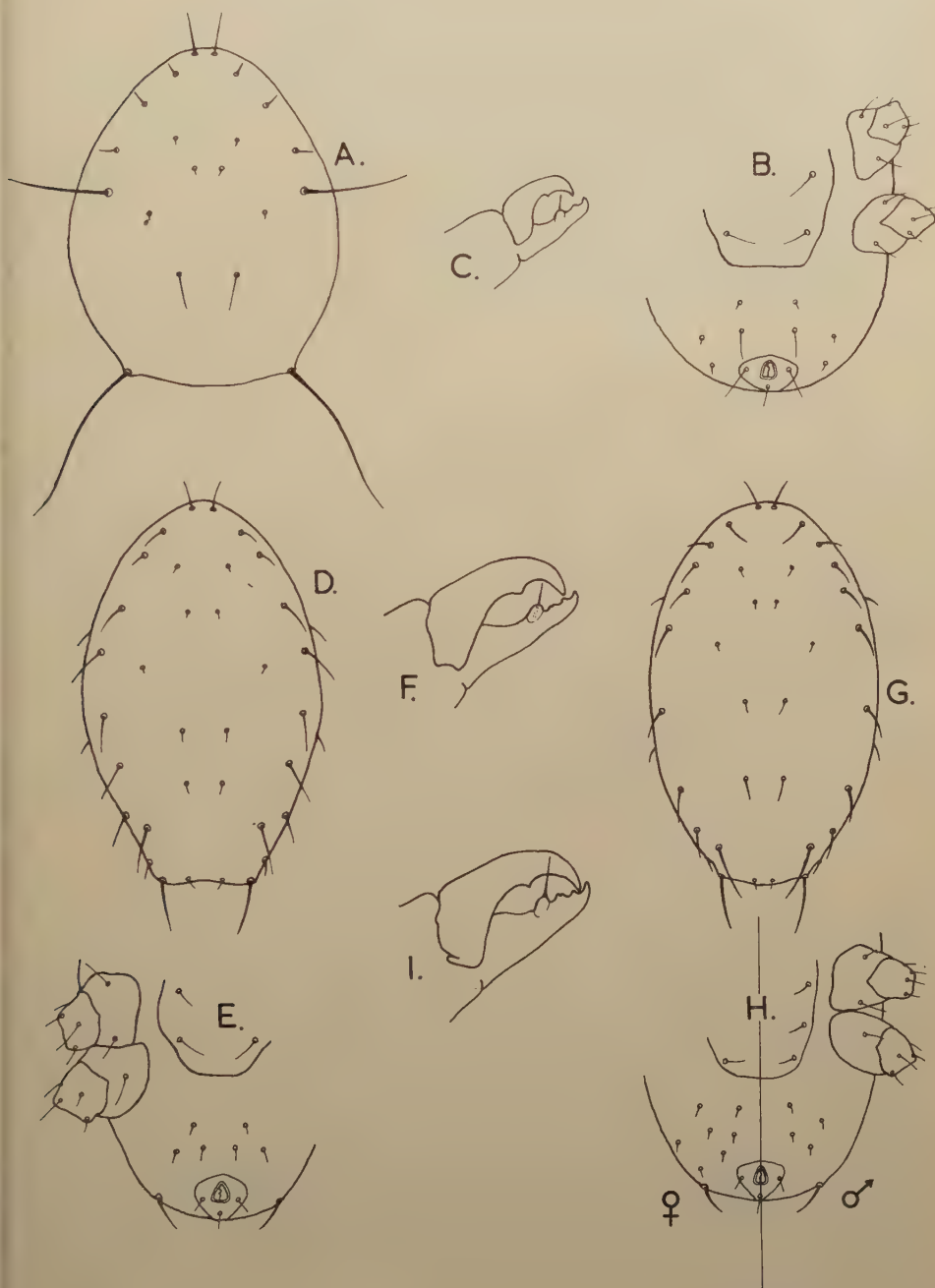


FIG. 9.—*Typhlodromus rhenanus*, immature stages. A, larva, dorsal; B, larva, ventral; C, larva, chelicera; D, protonymph, dorsal; E, protonymph, ventral; F, protonymph, chelicera; G, deutonymph, dorsal; H, deutonymph, ventral; I, deutonymph, chelicera.

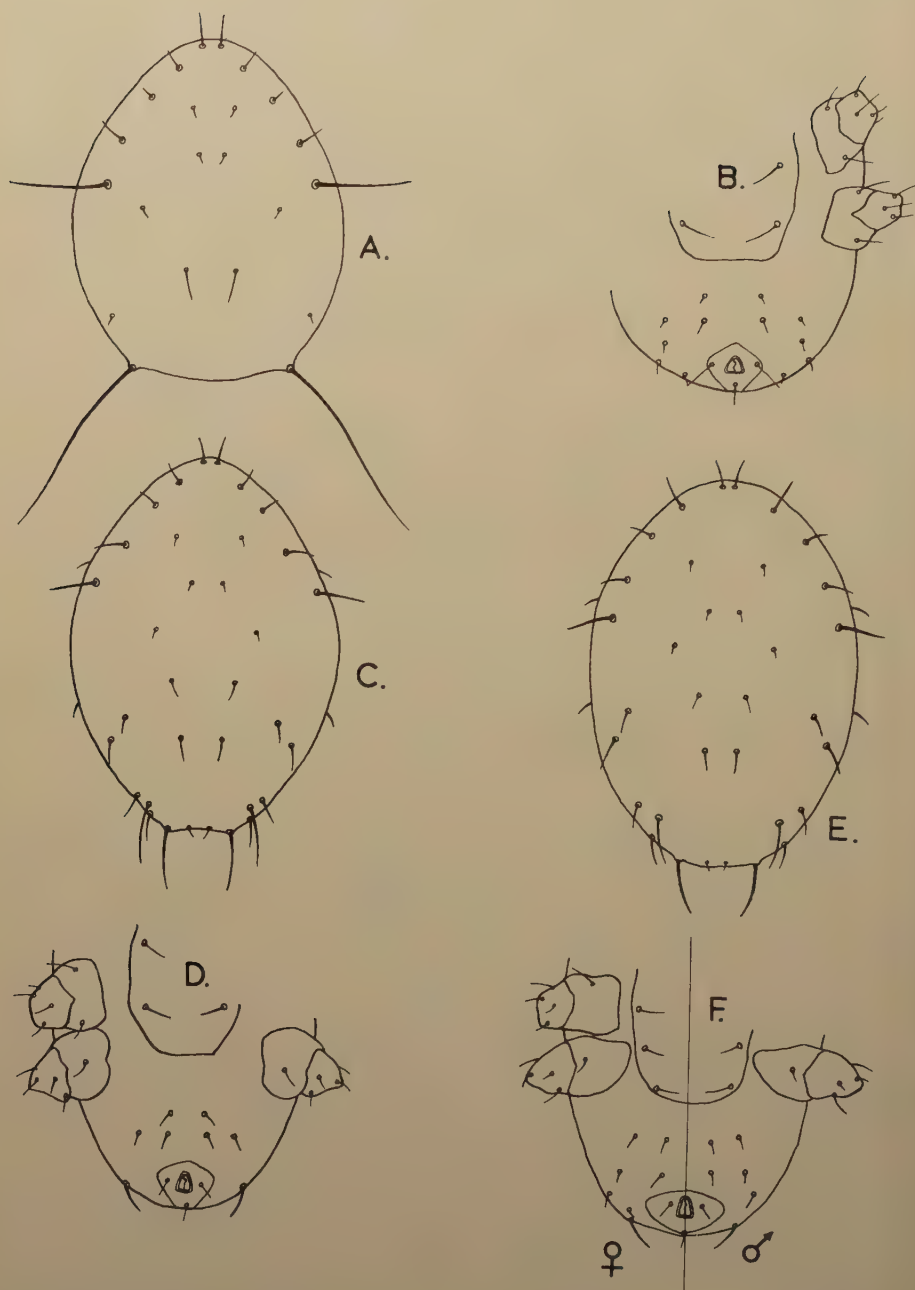


FIG. 10.—*Typhlodromus reticulatus*, immature stages. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

all, six pairs of setae surrounding anal plate. Movable digit of chelicera with one small tooth; fixed digit with one tooth and pilus dentilis.

Protonymph: length $165\ \mu$; width $115\ \mu$; single dorsal shield with 16 pairs of setae, eight in lateral row and L3 present. Setae located as in adult but posterior region compressed. Some setae longer in proportion to body than in adult. All setae smooth. Setae S1 and S2 on interscutal membrane. Setae surrounding anal plate reduced to four pairs. Sexes indistinguishable. Movable digit of chelicera with one small tooth; fixed digit with two teeth and pilus dentilis. Basi-tarsus IV with macroseta.

Deutonymph: length $201\ \mu$; width $120\ \mu$; dorsal shield with 16 pairs of setae. Without posterior compression but several setae longer in proportion to body than in adult. All setae smooth. Setae surrounding anal plate increased to seven pairs in female nymph, remaining at four in male. Movable digit of chelicera with one tooth; fixed digit with two teeth and pilus dentilis. Macroseta on basi-tarsus IV shorter than in protonymph.

Adult Stages (Figs 20 and 25).

Female: length $295\ \mu$; width $140\ \mu$; chaetotaxy as in deutonymph but many setae shorter in proportion to body. In summer, setae of lateral dorsal series slightly serrated but in winter more extreme. Ventrianal shield present with three pairs of setae in addition to para-anals. Shield of characteristic oblong shape. Movable digit of chelicera with one small tooth; fixed digit with two teeth and pilus dentilis. Macroseta on basi-tarsus IV shorter than in deutonymph.

Male: length $230\ \mu$; width $132\ \mu$; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with three pairs of setae in addition to para-anals. Fixed digit of chelicera with two teeth and pilus dentilis; movable digit with one small tooth and Y-shaped spermatophoral process.

The adult female of this species was described by Oudemans (1930*a* and *d*) and Nesbitt (1951). The male was described by Chant (1955), who established the synonymy of this species with *T. vitis* Oudemans and *Kampimodromus elongatus* (Oudemans).

***Typhlodromus rhenanus* (Oudemans, 1905).**

Immature Stages (Fig. 9).

Larva: length $155\ \mu$; width $112\ \mu$; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior dorsal shield with one pair long, whip-like setae. Seta D1 longer than L1, L2, or L3, which are of equal length. Seta D4 longer than all but D1, L4, or L5. Two pairs pre-anal setae present, the posterior long. Two pairs lateroventral setae present, both minute. In all, four pairs of setae surrounding anal plate. Movable digit of chelicera with one tooth; fixed digit with one tooth and pilus dentilis.

Protonymph: length $184\ \mu$; width $118\ \mu$; single dorsal shield with 17 pairs of setae, nine in lateral row, L3 absent. Other setae situated as in adult except for posterior compression. All setae smooth. Setae S1 and S2 on interscutal membrane. Four pairs of setae surrounding anal plate. Sexes indistinguishable. Movable digit of chelicera with one tooth; fixed digit with three teeth, the posterior two minute, and pilus dentilis.

Deutonymph: length $210\ \mu$; width $120\ \mu$; dorsal shield with 18 pairs of setae, 10 in lateral row, L3 present. Situated as in adult. Setae surrounding anal plate increased to eight pairs in female nymph, five pairs in male. Movable digit of chelicera with one tooth; fixed digit with three teeth, the posterior two minute, and pilus dentilis.

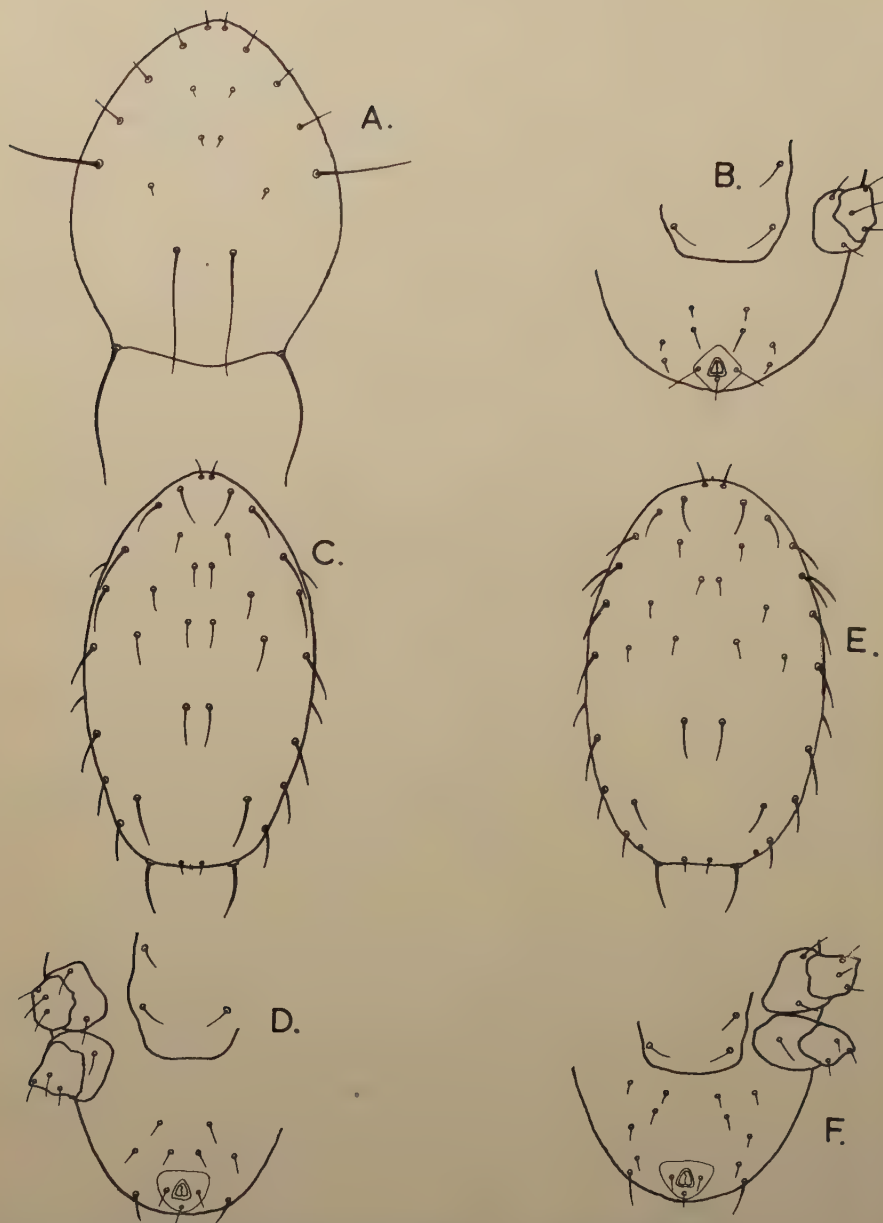


FIG. 11.—*Typhlodromus soleiger*, immature stages. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

Adult Stages (Figs 19 and 25).

Female: length 341 μ ; width 161 μ ; dorsal chaetotaxy as in deutonymph. In winter setae M2 and L10 may be serrated. Ventrianal shield present with four pairs of setae in addition to para-anals. Movable digit of chelicera with one tooth; fixed digit with three teeth and pilus dentilus.

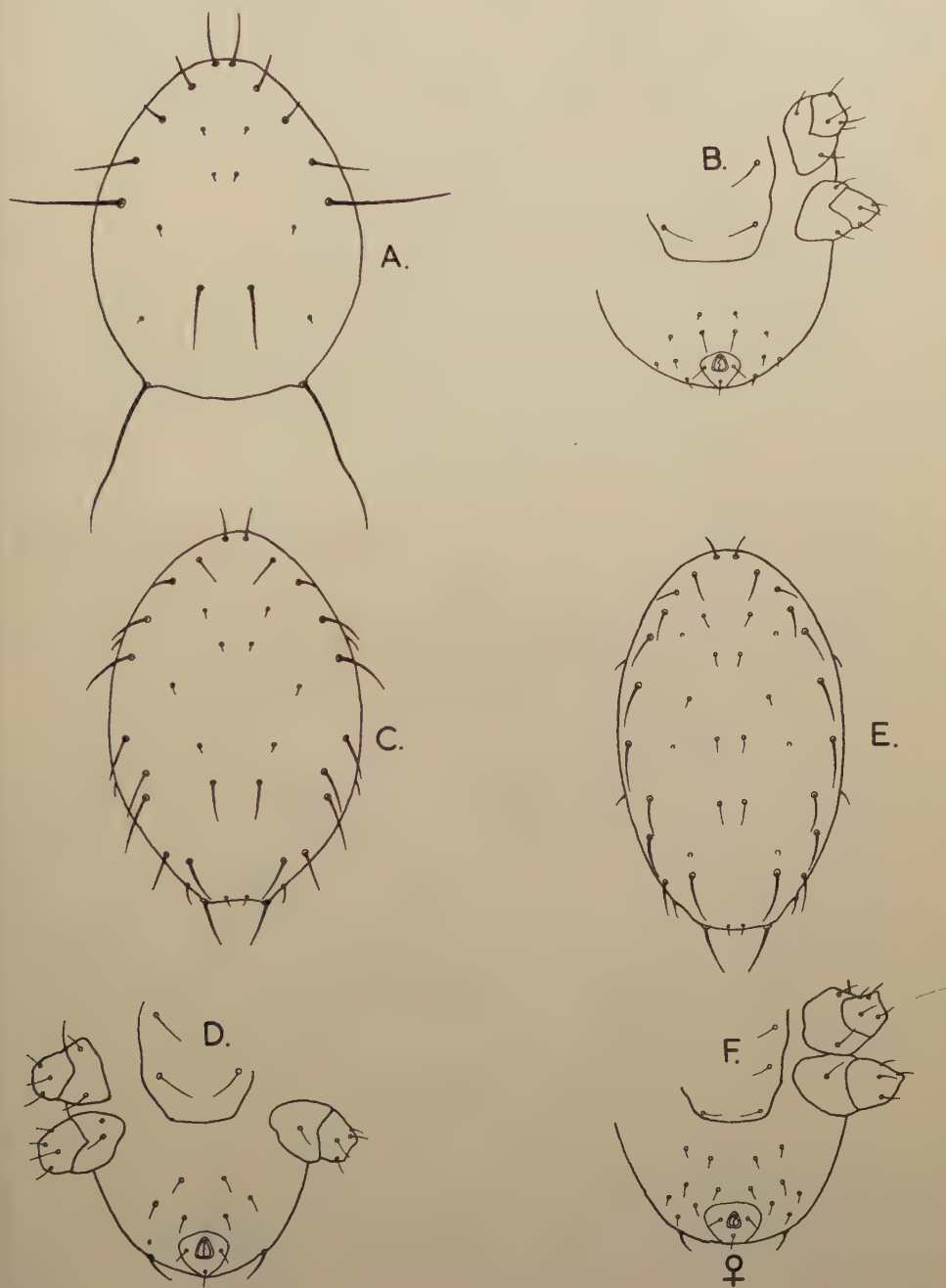


FIG. 12.—*Typhlodromus tiliarum*, immature stages. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

Male : length 259 μ ; width 137 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with four pairs of setae in addition to para-anals. Fixed digit of chelicera with two teeth and pilus dentilis ; movable digit with one tooth and spermatophoral process.

The adult forms of this species were described by Oudemans (1905 as *Seiulus rhenanus* ; 1915b as *Seiulus rhenanus* ; 1930c as *T. foenilis*), Nesbitt (1951), and Cunliffe & Baker (1953).

***Typhlodromus reticulatus* Oudemans, 1930.**

Immature Stages (Fig. 10).

Larva : length 168 μ ; width 115 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one minute pair of setae (in a few specimens two pairs were present) and one pair of long, whip-like setae. Seta D1 longer than L1, L2, or L3. Setae L1 and L3 approximately equal and twice as long as L2. Seta D4 shorter only than L4 and L5. Remaining setae minute. Two pairs of pre-anal setae present, the posterior longer. Two pairs lateroventral setae present, both minute. Postad are two pairs posteroventral setae, both minute. In all, six pairs of setae surrounding anal plate.

Protonymph : length 212 μ ; width 138 μ ; single dorsal shield with 17 pairs of setae, nine in lateral row and L3 present. Arranged as in adult except with posterior compression. Setae S1 and S2 on interscutal membrane. Four pairs of setae surrounding anal plate. Sexes indistinguishable.

Deutonymph : length 301 μ ; width 168 μ ; dorsal shield with 17 pairs of setae arranged as in adult, though longer in proportion to body. Setae surrounding anal plate increased to six pairs in the male nymph, seven pairs in the female.

Adult Stages (Figs 21 and 25).

Female : length 383 μ ; width 205 μ ; dorsal chaetotaxy as in deutonymph, except most setae shorter in proportion to body. Dorsum faintly reticulate. Ventrianal shield present with three pairs of setae in addition to para-anals.

Male : length 312 μ ; width 188 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with five pairs of setae in addition to para-anals.

The adult female of this species was described by Oudemans (1930c), Nesbitt (1951), Cunliffe & Baker (1953), and by Womersley (1954). Nesbitt, in Huffaker & Kennet (1953), is quoted as believing this species synonymous with *T. cucumeris* ; however, the larvae of these two species differ considerably and they seem to be separate and distinct species. The adult male of this species was described by Chant (1955).

***Typhlodromus soleiger* (Ribaga, 1902).**

Immature Stages (Fig. 11).

Larva : length 175 μ ; width 134 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair long, whip-like setae. Seta D1 shorter or equal in length to L1. Anterior lateral setae lengthen progressively to L4. Seta D4 approximately 10 times as long as L1. Remaining setae minute. Two pairs pre-anal setae present, the posterior longer. Two pairs lateroventral setae present, both minute. In all, four pairs of setae surrounding anal plate.

Protonymph : length 187 μ ; width 110 μ ; single dorsal shield with 18 pairs of setae, nine in lateral row, L3 absent. All dorsal setae longer in proportion to body

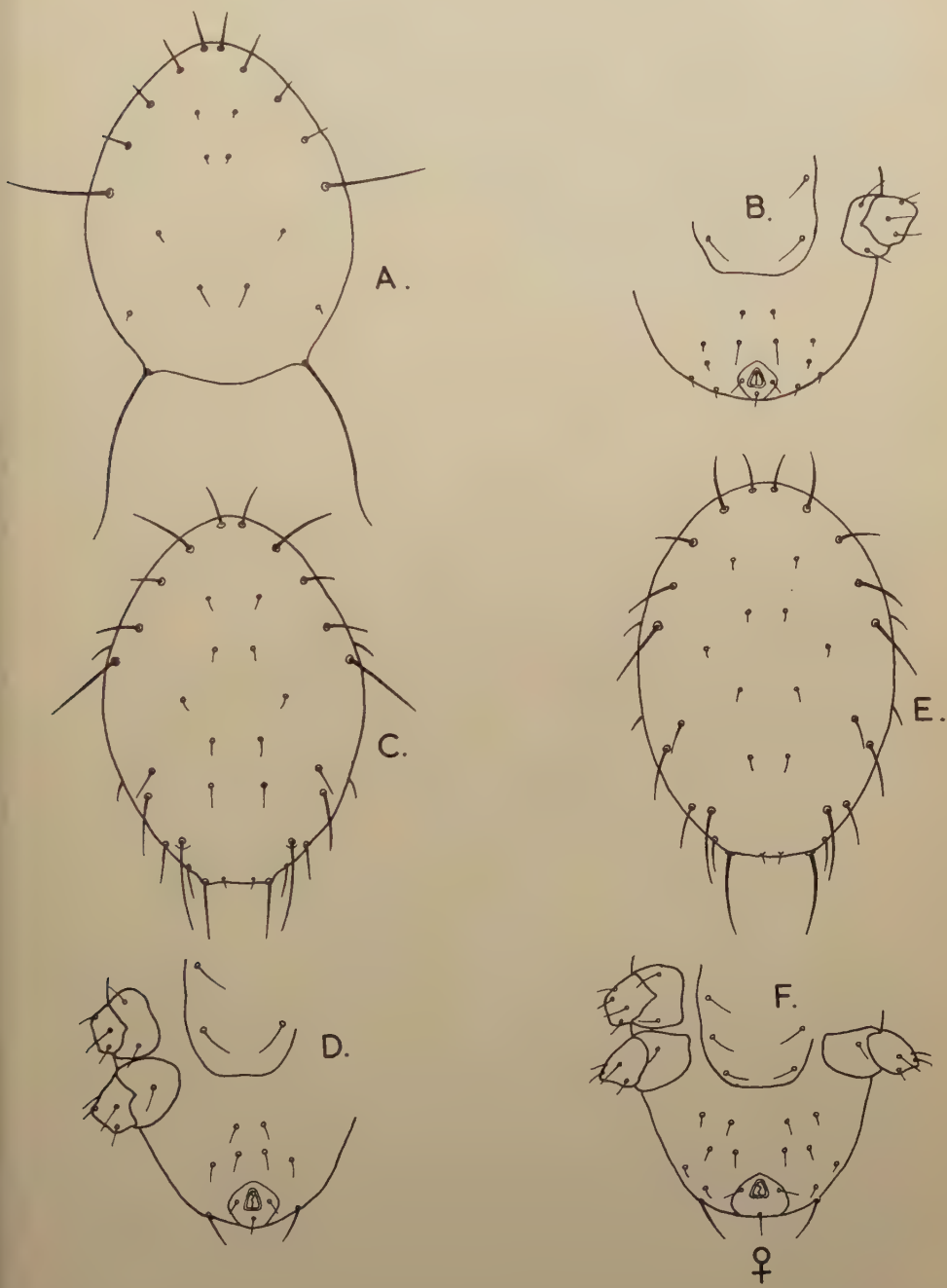


FIG. 13.—*Typhlodromus masseei*, immature stages. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

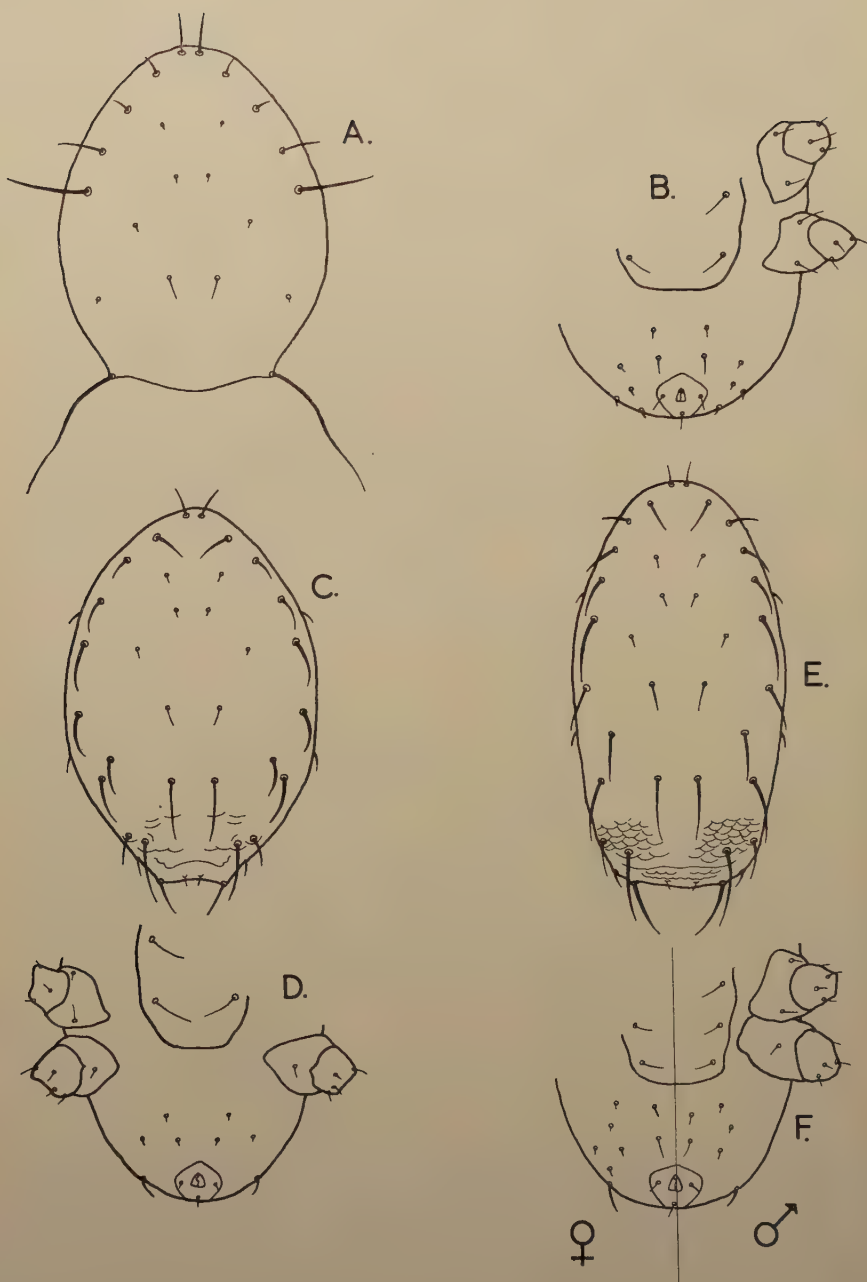


FIG. 14.—*Typhlodromus aceri*, immature stages. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

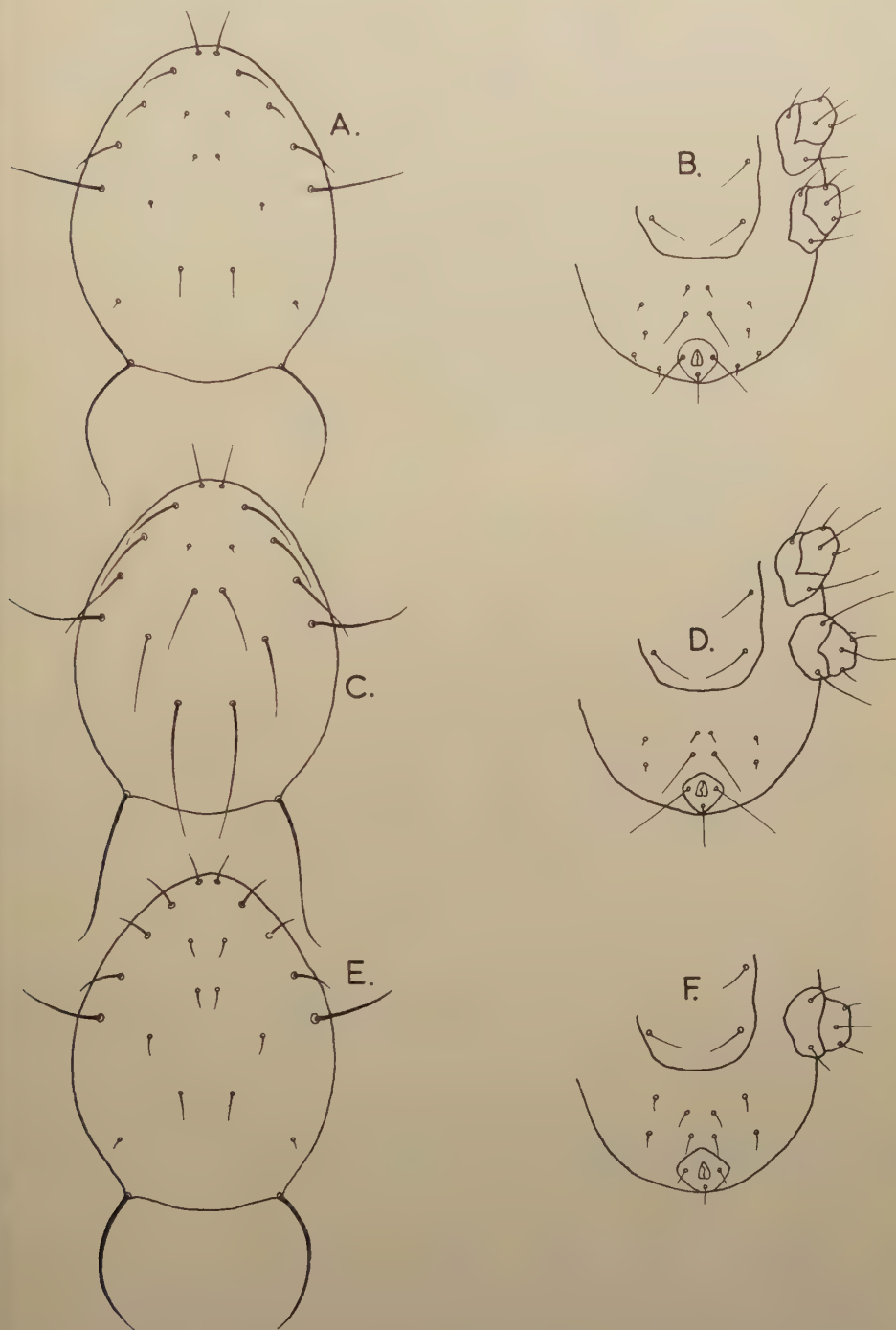


FIG. 15.—*Amblyseius graminis* larva; A, dorsal; B, ventral; *Typhlodromus occidentalis* larva; C, dorsal; D, ventral; *Typhlodromus cucumeris* larva (after MacGill, 1939); E, dorsal; F, ventral.

than in adult. Setae S1 and S2 on interscutal membrane. Four pairs of setae surrounding anal plate. Sexes indistinguishable.

Deutonymph : length 220 μ ; width 127 μ ; dorsal shield with 19 pairs of setae, 10 in lateral row, L3 present. Arranged as in adult. Setae surrounding anal plate increased to six pairs in female nymph, male not observed.

Adult Stages (Figs 21 and 25).

Female : length 345 μ ; width 150 μ ; dorsal chaetotaxy as in deutonymph. Unique in having three median (M) pairs of setae. Ventrianal shield of characteristic shape and with two pairs of setae in addition to para-anals.

Male : length 250 μ ; width 134 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with two pairs of setae in addition to para-anals.

The adult female of this species was described by Ribaga (1902 as *Seiulus soleiger*), and both sexes were described by Nesbitt (1951).

***Typhlodromus tiliarum* Oudemans, 1930.**

Immature Stages (Fig. 12).

Larva : length 150 μ ; width 103 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair of minute setae, and one pair of long, whip-like setae. Seta D1 longer than L1 or L2, shorter than L3. Seta L2 approximately one half as long as L1, which in turn is one half as long as L3. Seta D4 long, exceeded only by L4 and L6. Remaining setae minute. Two pairs of pre-anal setae present, the posterior longer. Two pairs lateroventral setae present, both minute. Two pairs posteroventral setae present, both minute. In all, six pairs of setae surround anal plate.

Protonymph : length 170 μ ; width 110 μ ; single dorsal shield with 18 pairs of setae, 10 in lateral row, L3 absent. All are longer in proportion to body than in adult, and posterior compression is evident. Setae S1 and S2 on interscutal membrane. Four pairs of setae surrounding anal plate. Sexes indistinguishable.

Deutonymph : length 234 μ ; width 120 μ ; dorsal shield with 19 pairs of setae, 11 in lateral row, L3 present. Arranged as in adult, and dorsum sometimes slightly reticulated. Three pairs of pores present in lateral row between dorsal (D) and lateral (L) setae. Setae surrounding anal plate increased to eight pairs in female nymph, male not observed.

Adult Stages (Figs 21 and 25).

Female : length 301 μ ; width 143 μ ; dorsal chaetotaxy as in deutonymph, dorsum slightly reticulated. Three pairs of pores prominent. Seta L10 located at a slight cleft in edge of shield. Ventrianal shield present with four pairs of setae in addition to para-anals.

Male : length 260 μ ; width 138 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with five pairs of setae in addition to para-anals.

The adult female of this species was described by Oudemans (1930b), and by Nesbitt (1951). The male was described by Chant (1955).

***Typhlodromus masseei* Nesbitt, 1951.**

Immature Stages (Fig. 13).

Larva : length 213 μ ; width 157 μ ; anterior dorsal shield with nine pairs of setae arranged as usual. Posterior shield with one pair of minute setae, and one pair of long, whip-like setae. Seta D1 slightly longer than L1, much longer than L2 and L3, which are of equal length. Seta D4 approximately equal in length to L2 and L3. Remaining setae minute. Two pairs of pre-anal setae present, the posterior

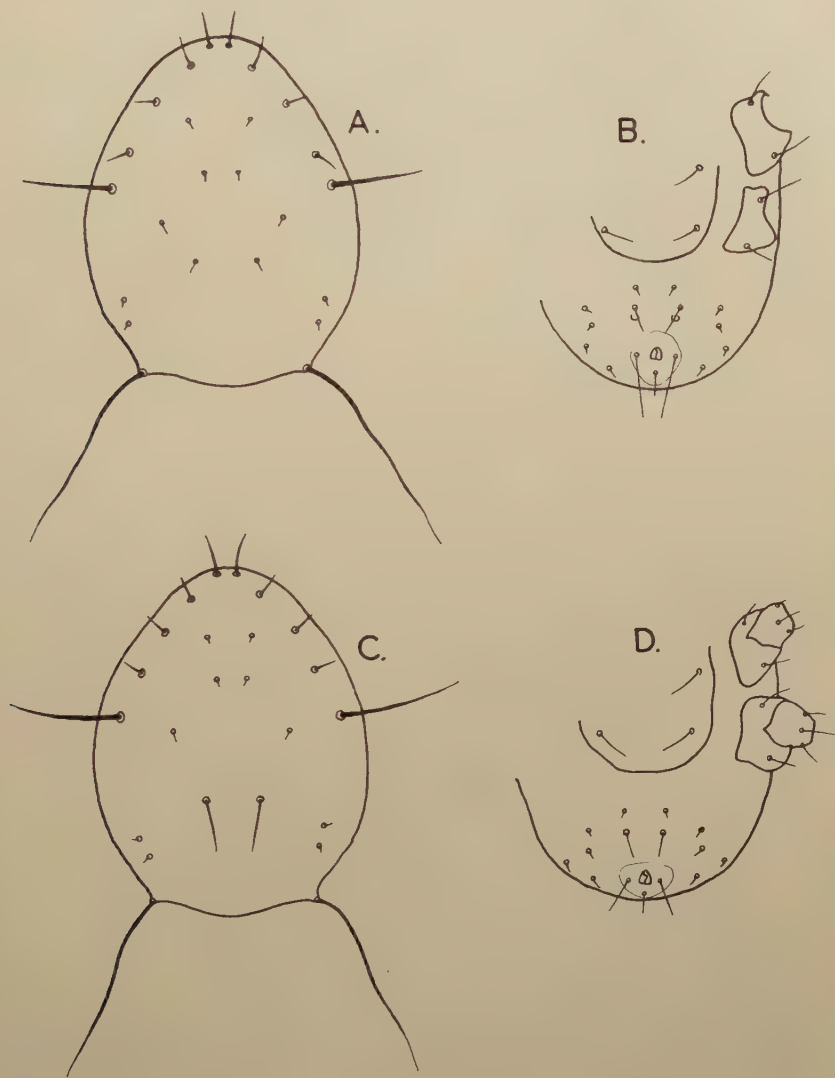


FIG. 16.—*Typhlodromus newsami* larva (after Evans, 1953); A, dorsal; B, ventral: *Typhlodromus marinus* larva; C, dorsal; D, ventral.

longer. Two pairs of lateroventral setae present, both minute. Two pairs of posteroventral setae present, both minute. In all, six pairs of setae surround anal plate.

Protonymph: length $225\ \mu$; width $159\ \mu$; single dorsal shield with 17 pairs of setae, nine in lateral row, L3 present. Setae arranged as in adult, but posterior compression evident. Setae L1, L3, and L4 much longer than distances between their bases. Seta L2 less than one half length L1, and less than distance between their bases. Setae S1 and S2 on interscutal membrane. Four pairs of setae surrounding anal plate. Sexes indistinguishable.

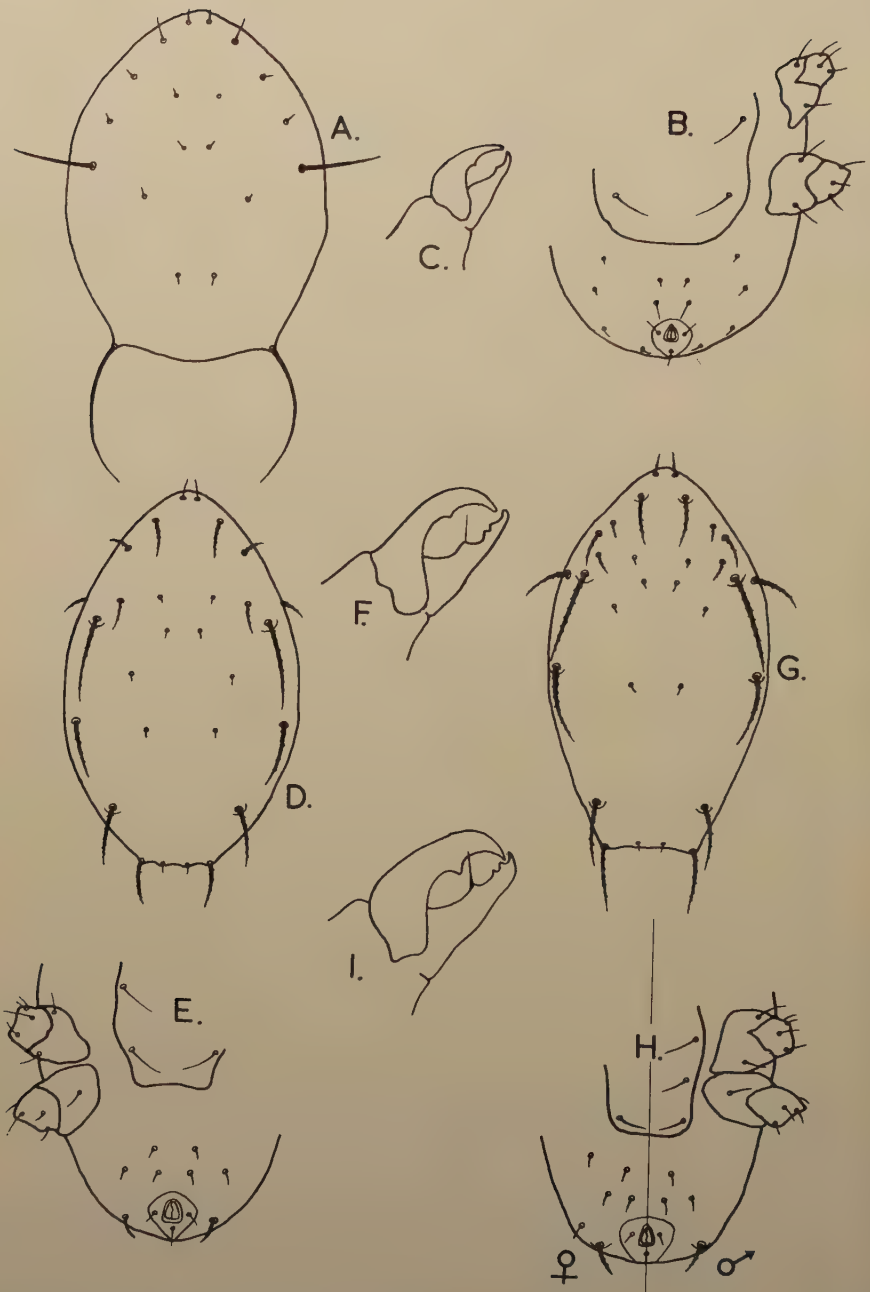


FIG. 17.—*Phytoseius macropilis*, immature stages. A, larva, dorsal; B, larva, ventral; C, larva, chelicera; D, protonymph, dorsal; E, protonymph, ventral; F, protonymph, chelicera; G, deutonymph, dorsal; H, deutonymph, ventral; I, deutonymph, chelicera.

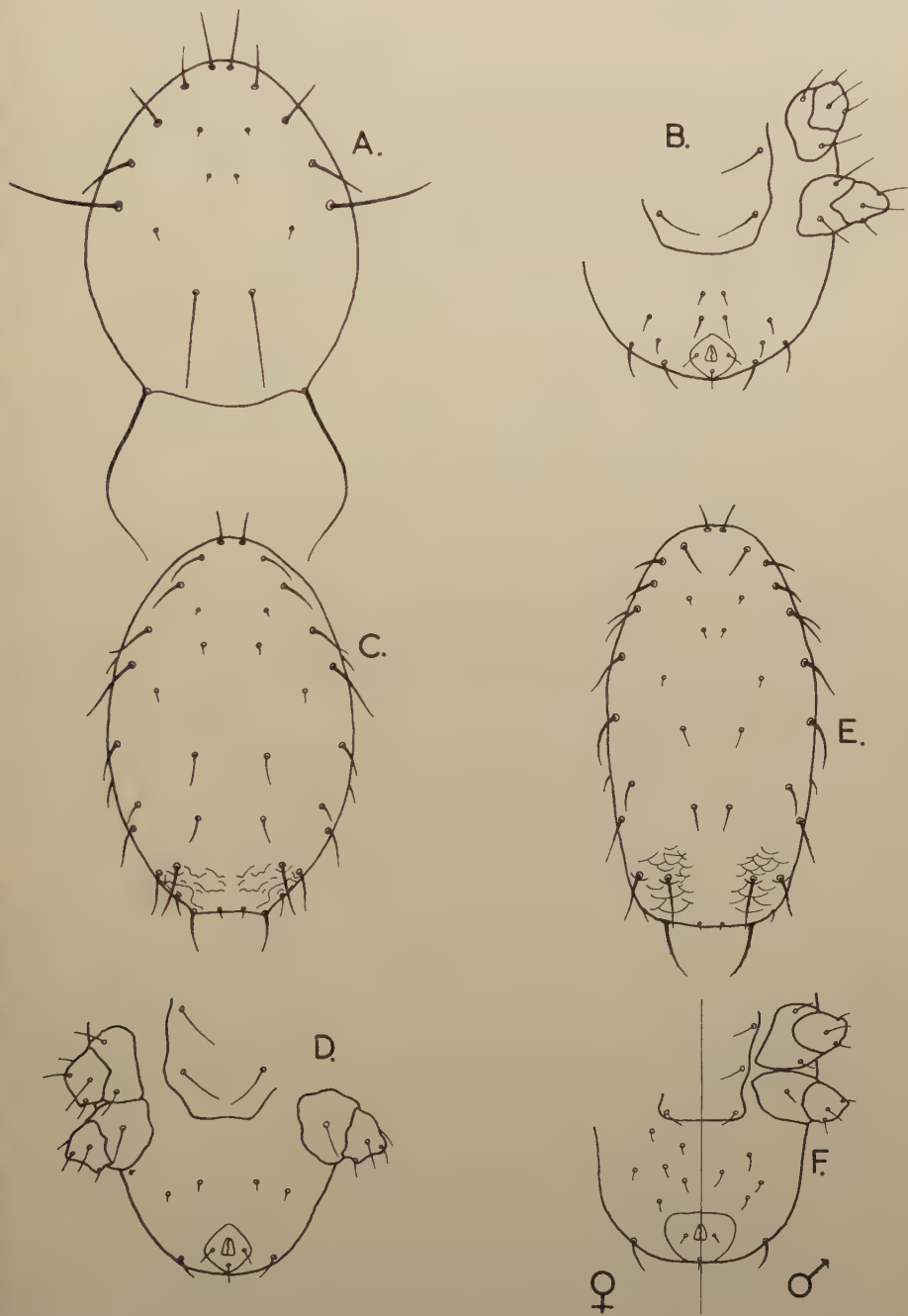


FIG. 18.—*Seirulus simplex*, immature stages. A, larva, dorsal; B, larva, ventral; C, protonymph, dorsal; D, protonymph, ventral; E, deutonymph, dorsal; F, deutonymph, ventral.

Deutonymph : length 435 μ ; width 220 μ ; dorsal shield with 17 pairs of setae arranged as in adult, but lateral setae longer in proportion to body than in female. Seta L2 shorter than other anterior laterals. Setae surrounding anal plate increased to seven pairs in female nymph, male not observed.

Adult Stages (Figs 22 and 25).

Female : length 490 μ ; width 268 μ ; dorsal chaetotaxy as in deutonymph, but most setae shorter in proportion to body. Seta L2 equalling L1 and L3 in length, and all anterior lateral setae longer than distances between their bases. Ventrianal shield present with three pairs of setae in addition to para-anals. A pair of pores may be present on shield.

Male : Not observed.

Both sexes of this species were described by Nesbitt (1951).

***Typhlodromus aceri* Collyer, 1957.**

Immature Stages (Fig. 14).

Larva : length 137 μ ; width 103 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair of minute setae, and one pair of long, whip-like setae. Seta D1 much longer than L1 or L2, and equal to L3. Setae L1 and L2 short and equal in length. Seta L3 more than one half as long as L4. D4 moderately long, longer than L1 or L2 but shorter than L3 or D1. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present, both minute. Two pairs of posteroventral setae present, both minute. In all, six pairs of setae surround anal plate.

Protonymph : length 170 μ ; width 106 μ ; single dorsal shield with 18 pairs of setae, 10 in lateral row, L3 absent. Setae as in adult, but most are longer in proportion to body. Posterior compression evident, and mild reticulation on posterior portions. Seta S1 and S2 on interscutal membrane. Four pairs of setae surrounding anal plate. Sexes indistinguishable.

Deutonymph : length 192 μ ; width 105 μ ; dorsal shield with 19 pairs of setae, 11 in lateral row, L3 present. Many lateral setae longer in proportion to body than in adult. All setae smooth, dorsal shield reticulated posteriorly. Setae surrounding anal plate increased to eight pairs in female nymph, six pairs in male.

Adult Stages (Figs 23 and 26).

Female : length 270 μ ; width 134 μ ; dorsal chaetotaxy as in deutonymph, but many setae shorter in proportion to body. Dorsum reticulated and in winter setae L9, L11, and M2 may be serrated. Ventrianal shield present with four pairs of setae in addition to para-anals.

Male : length 230 μ ; width 115 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of interscutal membrane. Ventrianal shield present with five pairs of setae in addition to para-anals.

***Typhlodromus cucumeris* Oudemans, 1930.**

Immature Stages (Fig. 15).

Larva : anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair of minute setae, and one pair of long, whip-like setae. Seta D1 shorter than L1, L2, or L3, these being approximately equal. Seta D4 equal to L1, L2, and L3. Remaining setae minute. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present. In all, four pairs of setae surrounding anal plate.

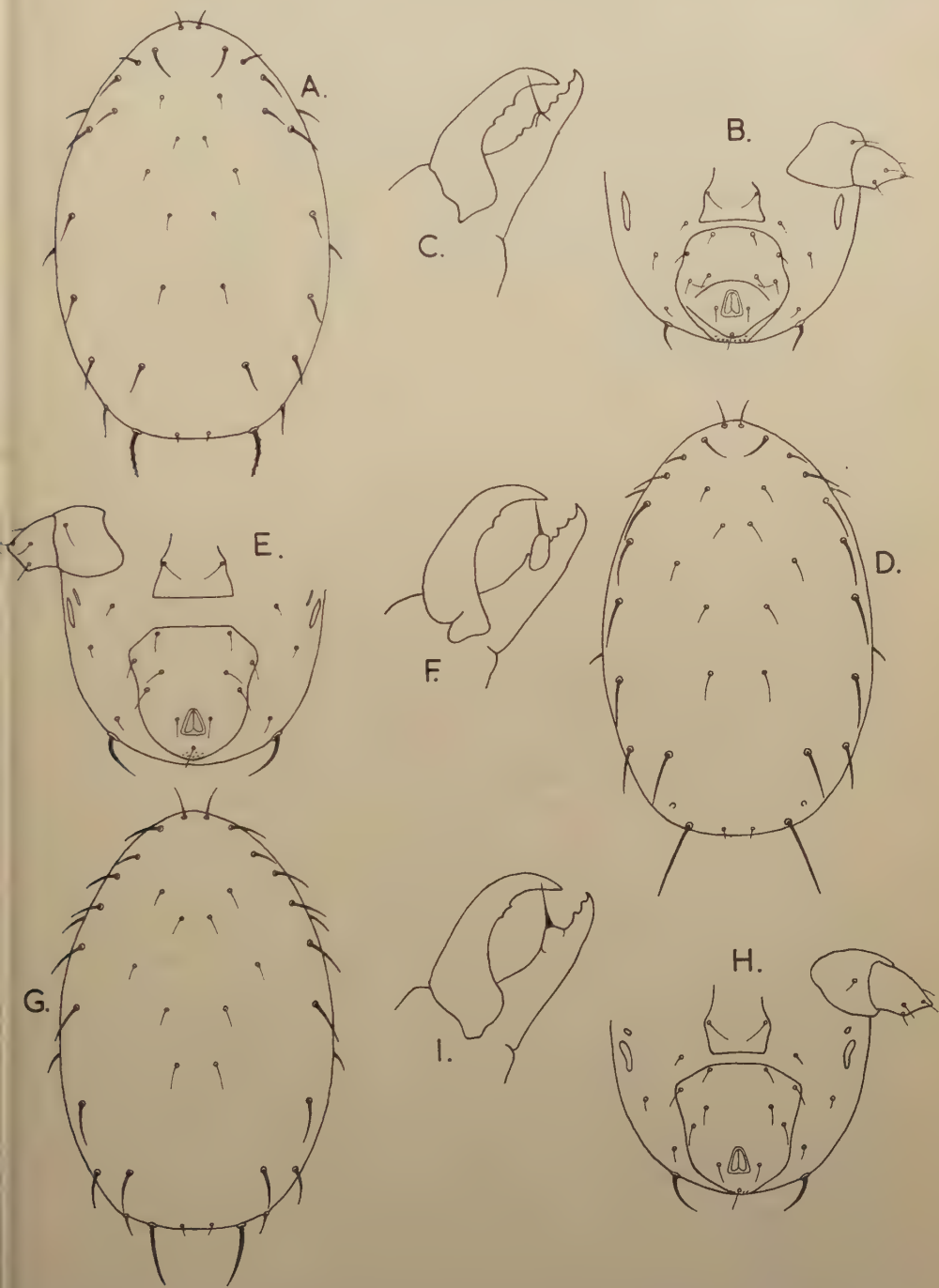


FIG. 19.—*Typhlodromus bakeri* female; A, dorsal; B, ventral; C, chelicera: *Typhlodromus tiliae* female; D, dorsal; E, ventral; F, chelicera: *Typhlodromus rhenanus* female; G, dorsal; H, ventral; I, chelicera.

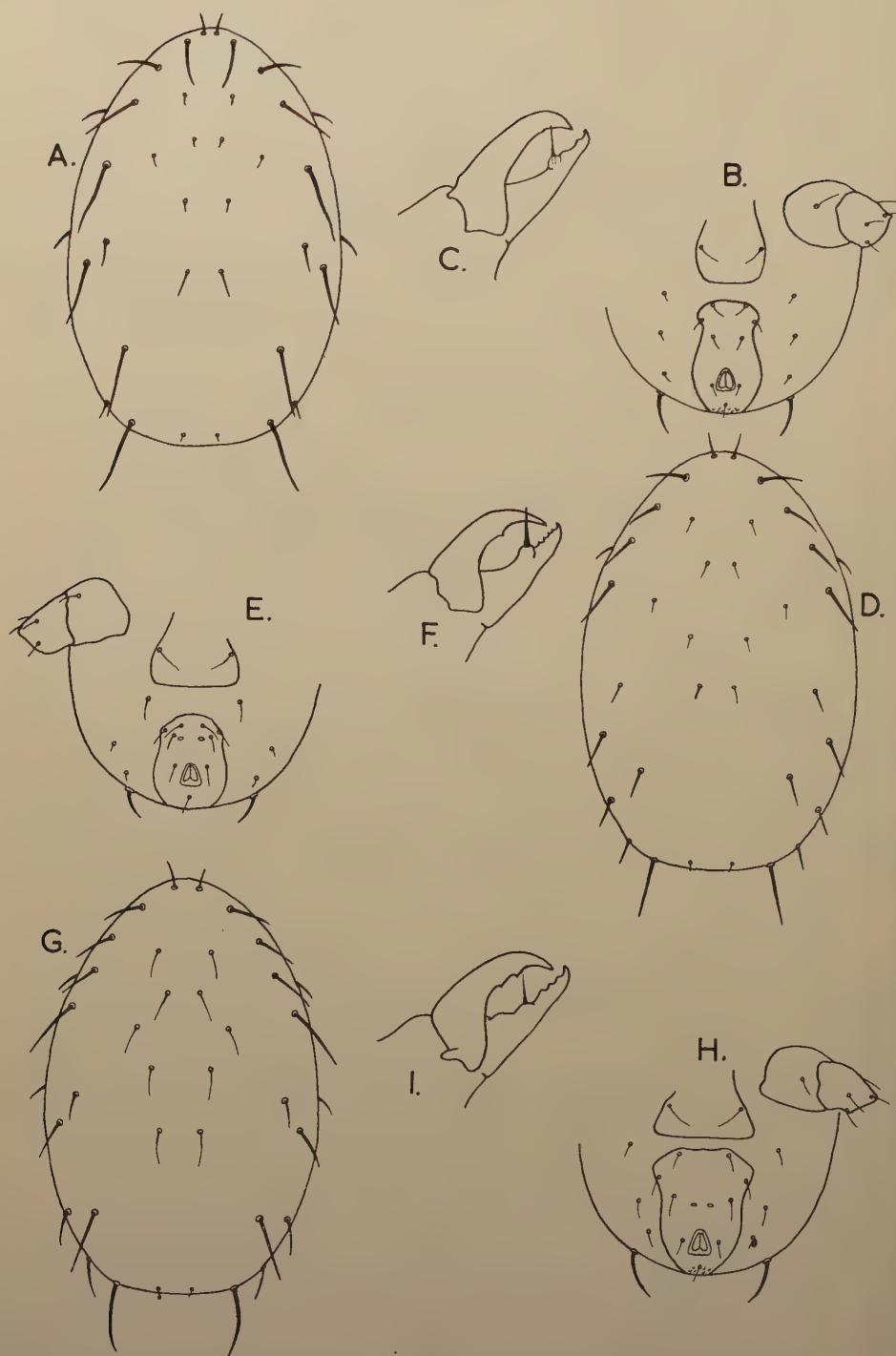


FIG. 20.—*Typhlodromus aberrans* female; A, dorsal; B, ventral; C, chelicera; *Typhlodromus finlandicus* female; D, dorsal; E, ventral; F, chelicera; *Typhlodromus umbraticus* female; G, dorsal; H, ventral; I, chelicera.

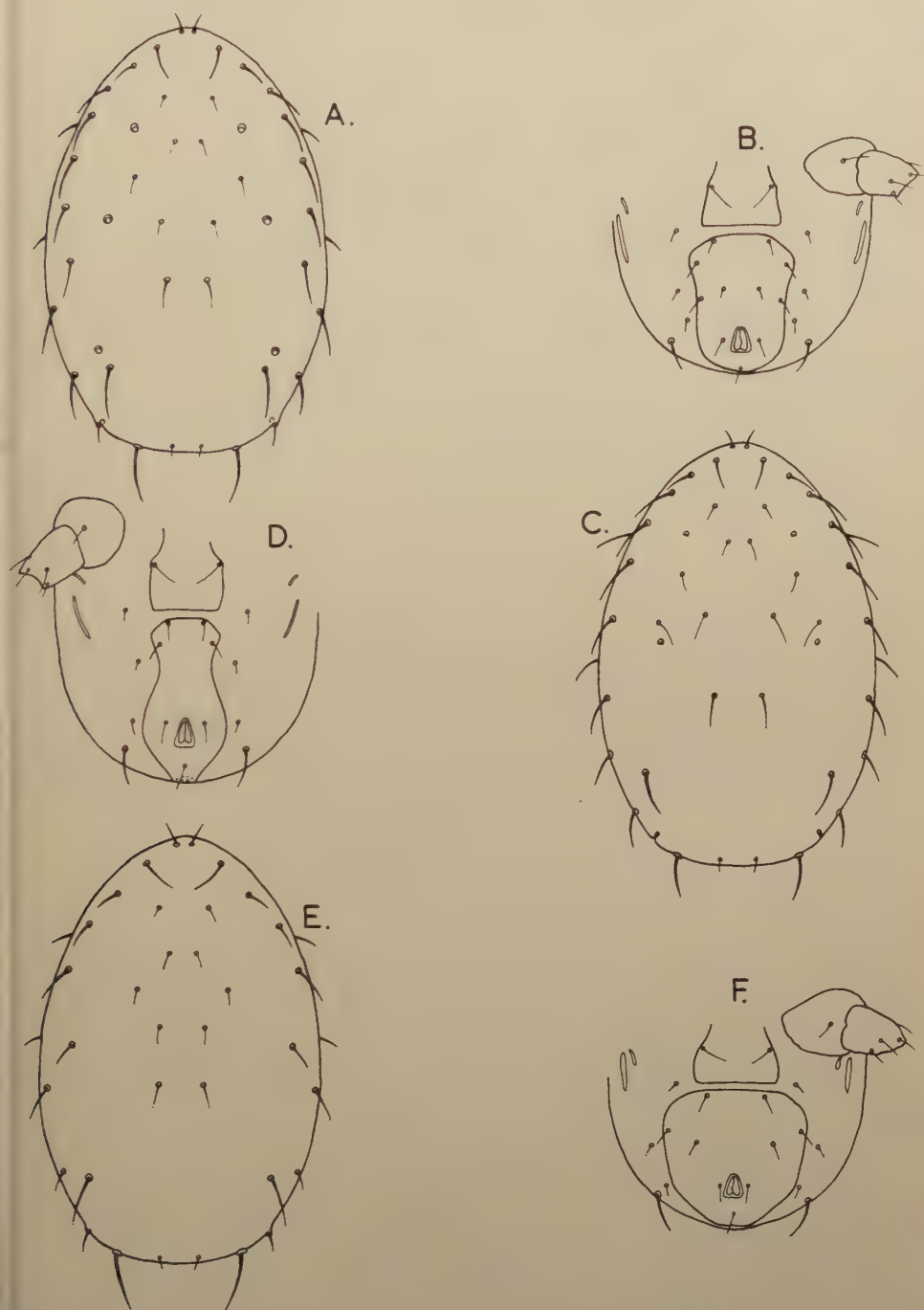


FIG. 21.—*Typhlodromus tiliarum* female; A, dorsal; B, ventral: *Typhlodromus soleiger* female; C, dorsal; D, ventral: *Typhlodromus reticulatus* female; E, dorsal; F, ventral.

From Miss MacGill's (1939) drawings of *T. thripsi*, a synonym, the exact relationship between the lengths of D1, L1, L2, and L3 cannot be determined.

Protonymph : Nothing can be determined from Miss MacGill's drawing of the dorsum of this stage. Ventrally, four pairs of setae surround anal plate.

Deutonymph : Miss MacGill did not draw this stage and it has not been observed by the present author.

Adult Stages (Figs 22 and 25).

Female : length 321 μ ; width 237 μ ; dorsal shield with 17 pairs of setae, nine in lateral row. Setae S1 and S2 on interscutal membrane. Ventrianal shield present with three pairs of setae in addition to para-anals. Four pairs of setae surrounding ventrianal shield, and in all seven pairs of setae, exclusive of para-anals, are present on posteroventral surface.

Male : length 270 μ ; width 181 μ ; dorsal chaetotaxy as in female, except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with three pairs of setae in addition to para-anals.

The above description of immature stages was largely taken from MacGill (1939) ; during the present study not enough mites of this species were collected to enable rearing and redescription. Measurements were not given by Miss MacGill.

The adult female of this species was described by Oudemans (1930c), MacGill (1939), Nesbitt (1951), Cunliffe & Baker (1953), and Womersley (1954). The male was described by MacGill (loc. cit.).

***Typhlodromus marinus* (Willmann, 1952).**

Immature Stages (Fig. 16).

Larva : length 160 μ ; width 118 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with two pairs of minute setae and one pair of long, whip-like setae. Seta D1 longer than L1, L2, or L3, which are short. Seta L3 as long as L1. Seta D4 longer than other dorsal setae except L4 and L7. Remaining setae minute. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present, both minute. Two pairs of posteroventral setae present, both minute. In all, six pairs of setae surround anal plate.

Protonymph : length 225 μ ; width 134 μ ; chaetotaxy as in *T. reticulatus*.

Deutonymph : length 285 μ ; width 171 μ ; chaetotaxy as in *T. reticulatus*.

Adult Stages (Figs 22 and 25).

Female : length 335 μ ; width 201 μ ; chaetotaxy as in *T. reticulatus* except ventrianal shield longer than broad, and lateral setae of dorsal shield shorter.

Male : length 282 μ ; width 137 μ ; chaetotaxy as in *T. reticulatus* except lateral setae of dorsal shield shorter.

The adult female of this species was described by Willmann (1952) as *Lasioseius marinus*. It was transferred to the present genus by Chant (1956). The male has not previously been described.

***Typhlodromus occidentalis* Nesbitt, 1951.**

Larval Stage (Fig. 15).

Only the larva of this species, indigenous to North America, has been examined by the present author.

Larva : length 132 μ ; width 105 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with a single pair of long, whip-like setae. Seta D1 slightly shorter than L1 or L2, which are equal. Seta L3 more than one half as long as L4. Setae D3, D4, and M1 extremely long, D4

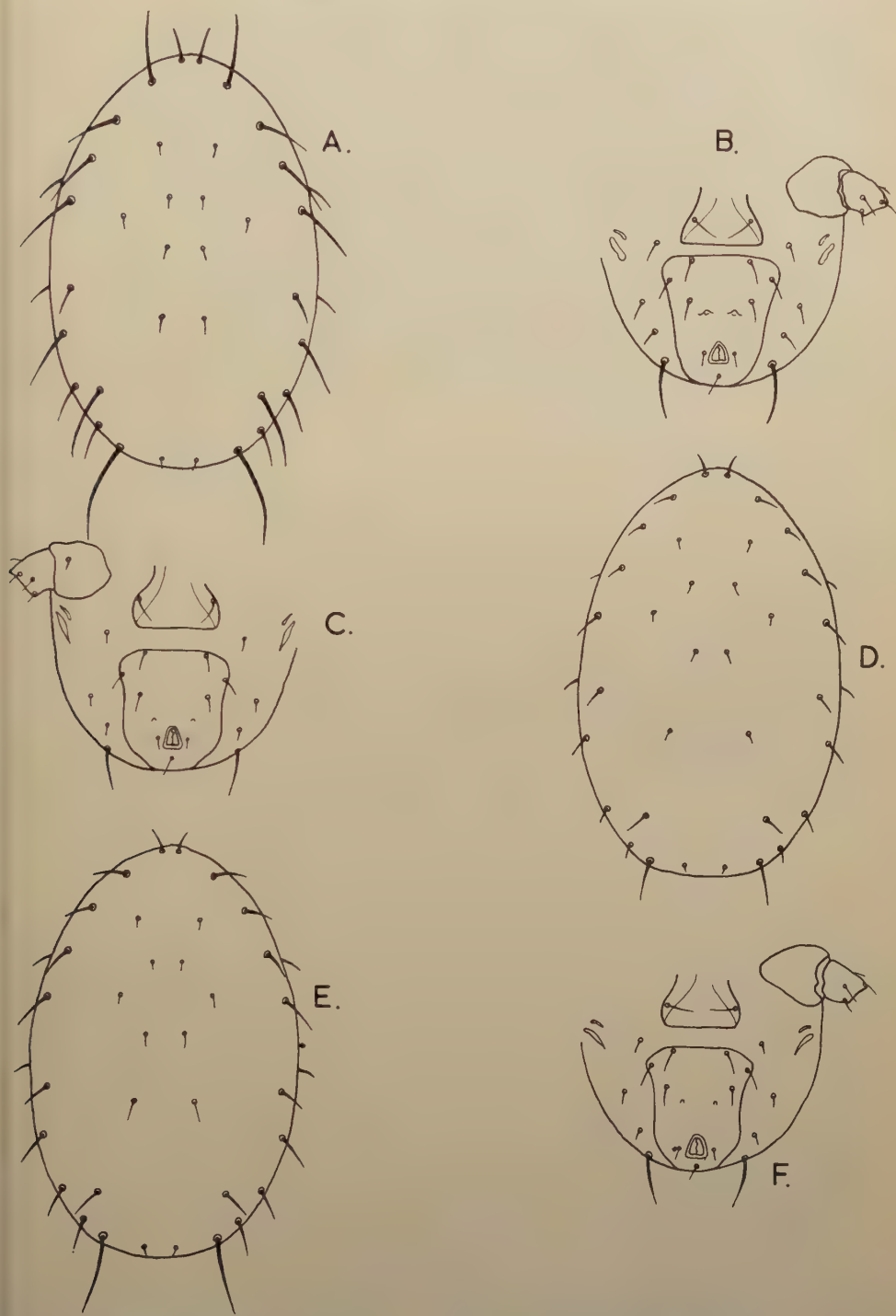


FIG. 22.—*Typhlodromus masseei* female; A, dorsal; B, ventral; *Typhlodromus marinus* female; D, dorsal; C, ventral; *Typhlodromus cucumeris* female; E, dorsal; F, ventral.

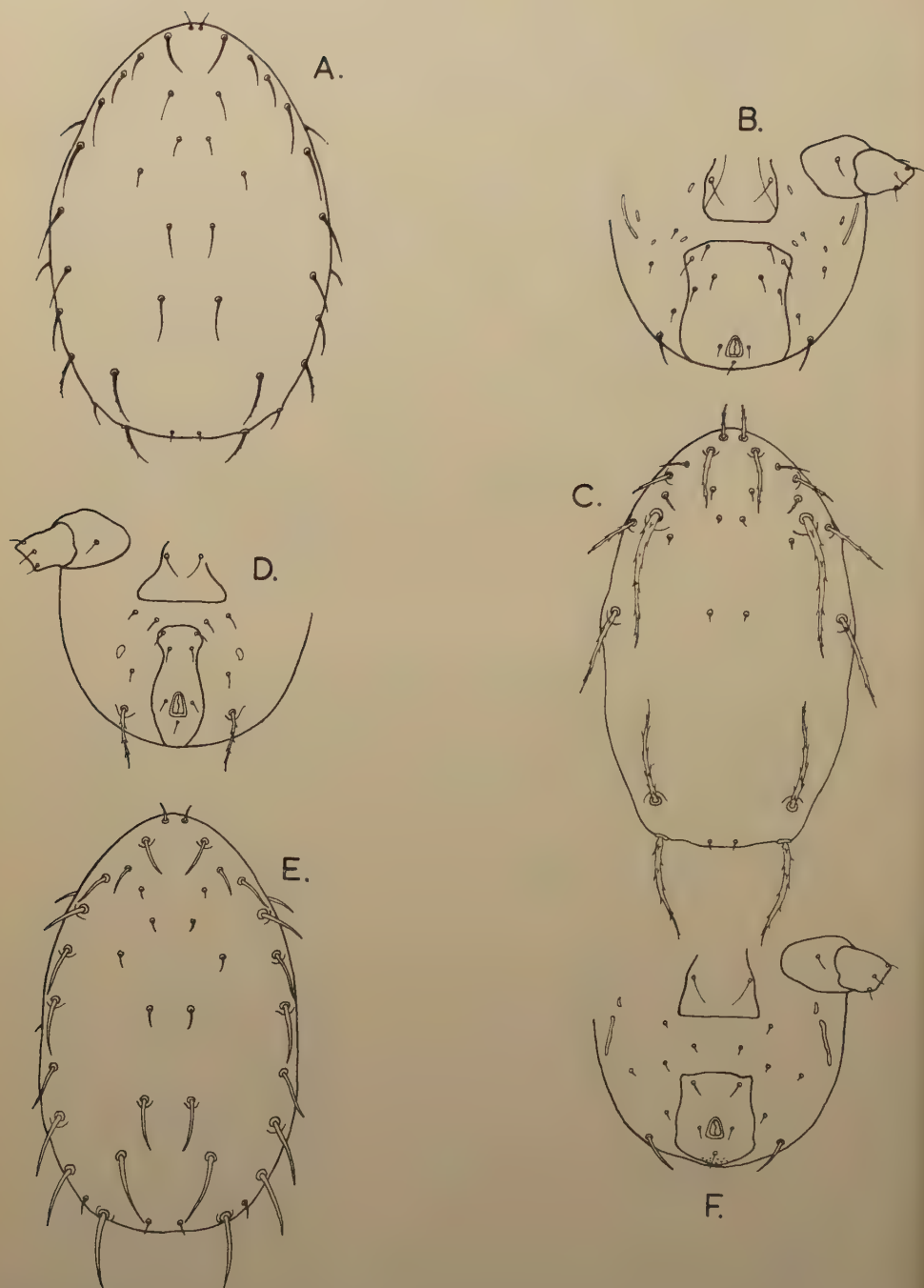


FIG. 23.—*Typhlodromus aceri* female; A, dorsal; B, ventral; *Phytoseius macropilis* female; C, dorsal; D, ventral; *Seiulus simplex* female; E, dorsal; F, ventral.

being the longest on the dorsal surface. Seta D2 is the only minute seta on dorsal surface. Para-anal setae very long, extending well beyond posterior margin of body. Two pairs of pre-anal setae present, the posterior being long and extending beyond the anus. Two pairs of lateroventral setae present, both minute. In all, four pairs of setae surrounding anal plate. Setae on larval coxae also of extreme length.

The adult female of this species was described by Nesbitt (1951).

Typhlodromus newsami Evans, 1953.

Larval Stage (Fig. 16).

The following description is from Evans (1953). The species is indigenous to Malaya, and only the larva is described here.

Larva : anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with two pairs of minute setae, and one pair of long, whip-like setae. Seta D1 longer than L1, L2, or L3, L2 and L3 being minute. Seta D4

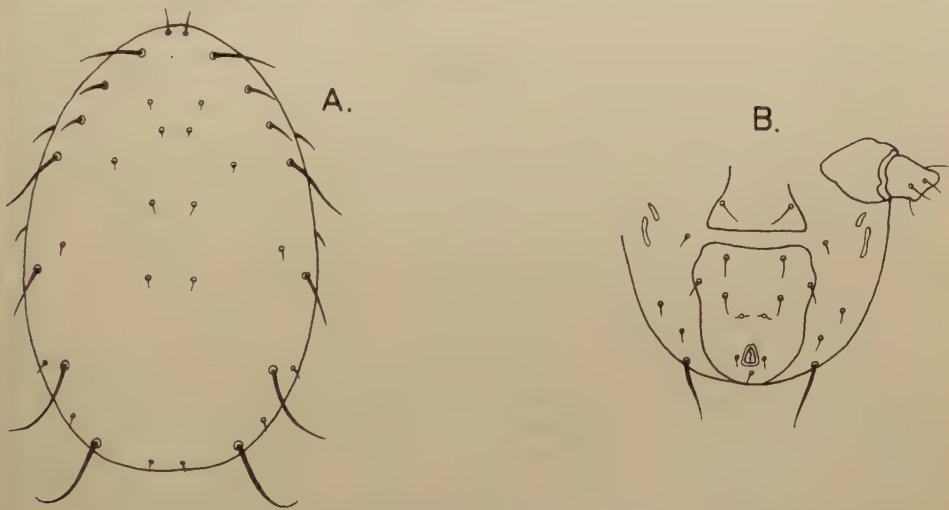


FIG. 24.—*Amblyseius graminis* female; A, dorsal; B, ventral.

minute. Lateral para-anal setae long, extending beyond posterior margin of body. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present, both minute. Postad are two pairs posteroventral setae, both minute. In all, six pairs of setae surrounding anal plate. A pair of pores is present behind pre-anal setae.

The males and females of this species were described by Evans (1953).

Phytoseius macropilis (Banks, 1909).

Immature Stages (Fig. 17).

Larva : length 139 μ ; width 107 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair of long, whip-like setae. Setae D1, L2, L3, M1, and the dorsal (D) setae minute. Seta L1 twice as long as all but L4. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present, both minute. Two pairs of posteroventral setae present, both minute. In all, six pairs of setae surrounding anal plate. Movable digit of chelicera with a single tooth ; fixed digit with one tooth. No pilus dentilis observed.

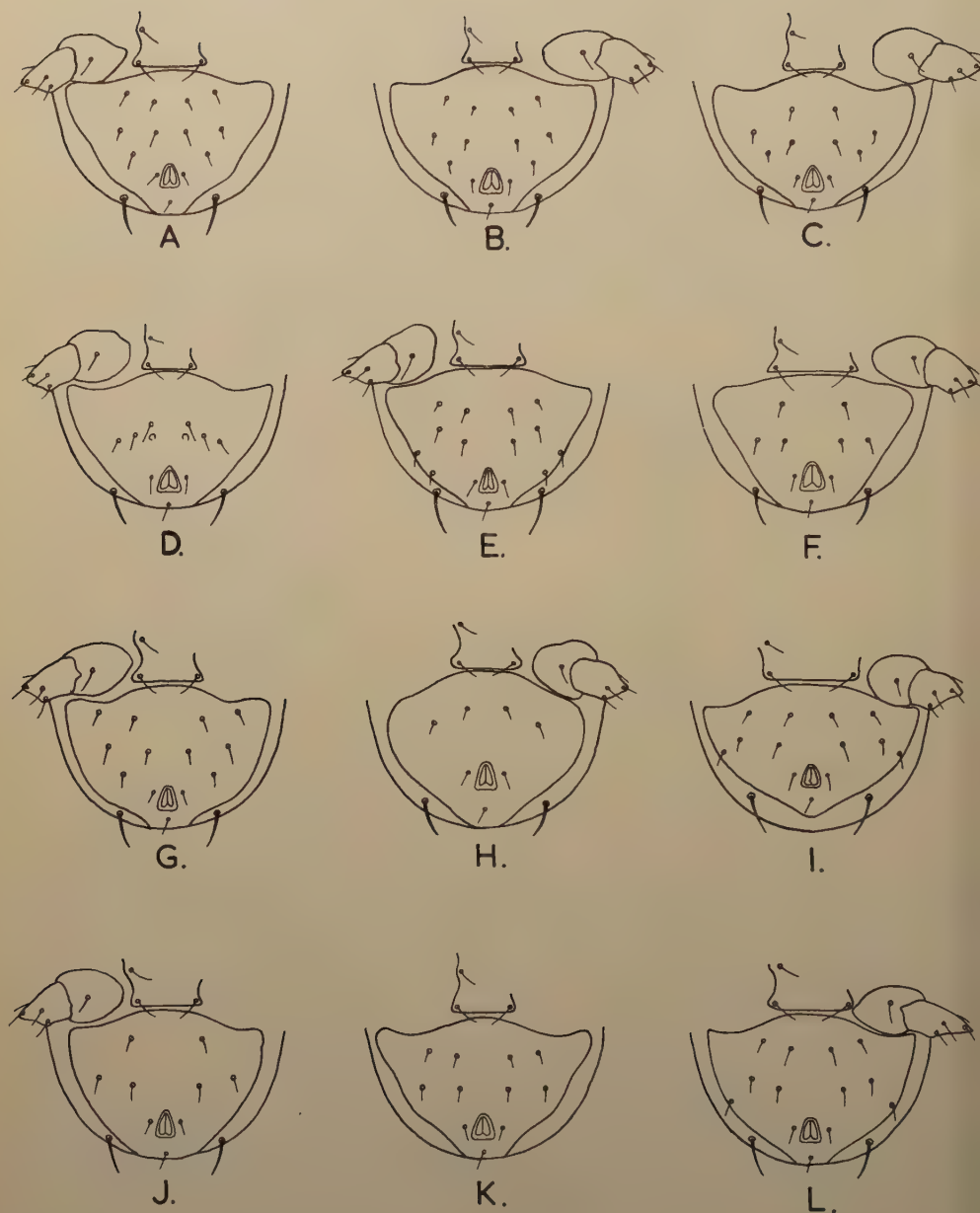


FIG. 25.—Ventrianal shield of adult males. A, *T. bakeri*; B, *T. tiliae*; C, *T. rhenanus*; D, *T. finlandicus*; E, *T. umbraticus*; F, *T. aberrans*; G, *T. tiliarum*; H, *T. soleiger*; I, *T. reticulatus*; J, *T. cucumeris*; K, *T. masseei*; (after Nesbitt, 1951); L, *T. marinus*.

Protonymph: length 186 μ ; width 118 μ ; single dorsal shield with 14 pairs of setae, S1 appearing on shield, S2 and L3 absent. Seta D5 absent in all stages. Seta L5 prominent and on a slight protuberance. Seta L4 mesad of L5. All lateral setae, D1 and S1 serrated. Four pairs of setae surrounding anal plate. Sexes indistinguishable. Movable digit of chelicera with one tooth; fixed digit with two teeth and pilus dentilis.

Deutonymph: length 230 μ ; width 127 μ ; dorsal shield with 15 pairs of setae. L3 present. Setae generally less prominent than in adult. All lateral setae, D1 and S1 serrated. Setae L5 and M2 on protuberances. Six pairs of setae surrounding anal plate of female nymph, four of male. Movable digit of chelicera with one tooth; fixed digit with two teeth and pilus dentilis.

Adult Stages (Figs 23 and 26).

Female: length 304 μ ; width 159 μ ; dorsal chaetotaxy as in deutonymph except lateral setae and M2 longer and more prominent. All laterals, D1 and S1 strongly serrated. Ventrianal shield present with two pairs of setae in addition to para-anals. This matter is contentious; Womersley (1954) collected two specimens of this species in Australia with three pairs of setae on the ventrianal shield and concluded that earlier authors were in error. However, the present author reared from a single female specimen individuals with either two or three setae here, and even individuals with two on one side and three on the other. Apparently the species is variable in this respect, though the total number of setae present on the posterior ventral surface is always constant.

Male: length 250 μ ; width 123 μ ; chaetotaxy as in female. Ventrianal shield present with three pairs of setae in addition to para-anals.

Both sexes of this species were described by Banks (1909 as *Sejus macropilis*), Oudemans (1915a and b as *Seiulus spoofi*), Nesbitt (1951 as *P. spoofi* and 1954 as *P. macropilis*), Cunliffe & Baker (1953), and Womersley (1954). This species can easily be confused with *P. plumifer* (C. & F.) 1876 and Nesbitt considered them synonymous. However, the author has examined specimens of *P. plumifer* in the Berlese collection at Florence, Italy, and observed that this, unlike *P. macropilis*, possesses seta D5, though in all other respects the two are identical. Berlese's specimens are not types but it may be assumed that he had access to the collections of Canestrini and Fanzago when he identified them.

Seiulus simplex Chant, 1956.

Immature Stages (Fig. 18).

Larva: length 159 μ ; width 120 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair of long, whip-like setae. Seta D1 more than twice as long as L1. Seta L2 longer than L1, but shorter than L3. Seta D4 exceedingly long, extending almost to posterior margin of body. Other setae minute. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present, both minute. Two pairs of posteroventral setae present, of moderate length. In all, six pairs of setae surrounding anal plate.

Protonymph: length 163 μ ; width 127 μ ; single dorsal shield with 18 pairs of setae, 10 in lateral row, L3 absent. Posterior compression evident. Setae S1 and S2 on interscutal membrane. All setae longer in proportion to body than in adult. Three pairs of setae surrounding anal plate. Sexes indistinguishable.

Deutonymph: length 236 μ ; width 150 μ ; dorsal shield with 19 pairs of setae, L3 present. Some areas reticulated. Seven pairs of setae surrounding anal plate in female nymph, five in male.

Adult Stages (Figs 23 and 26).

Female: length 330 μ ; width 180 μ ; dorsal chaetotaxy as in deutonymph. Dorsum reticulated, especially in winter form. Ventrianal shield present with only two pairs of setae in addition to para-anals.

Male: length 298 μ ; width 147 μ ; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with four pairs of setae in addition to para-anals.

The adult forms of this species were described by Chant (1956).

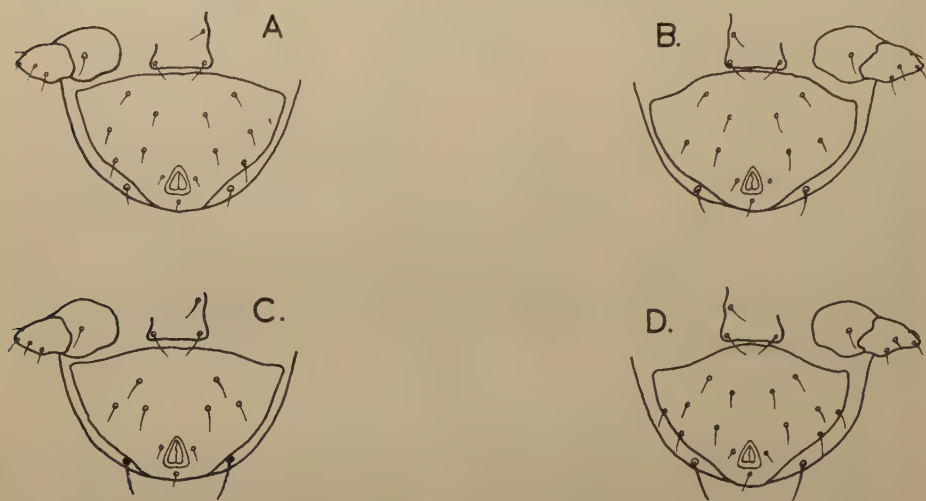


FIG. 26.—Ventrianal shields of adult males. A, *T. aceri*; B, *S. simplex*; C, *P. macropilis*; D, *A. graminis*.

Amblyseius graminis* Chant, 1956.Immature Stages.*

Larva (Fig. 15): length 200 μ ; width 125 μ ; anterior dorsal shield with nine pairs of setae arranged as usual for the genus. Posterior shield with one pair of minute setae and one pair of long, whip-like setae. Seta D1 longer than L1 or L2, L2 shorter than L1. Seta L3 longer than L1. Seta D4 longer than L2 but equal to or shorter than L1. Lateral para-anal setae extending beyond posterior margin of body. Two pairs of pre-anal setae present, the posterior longer. Two pairs of lateroventral setae present, both minute. Two pairs of posteroventral setae present, both minute. In all, six pairs of setae surrounding anal plate.

Protonymph: length 205 μ ; width 136 μ ; single dorsal shield with 17 pairs of setae, nine in lateral row, L3 present. All lateral setae longer in proportion to body than in adult. Four pairs of setae surrounding anal plate. Sexes indistinguishable. Setae S1 and S2 on interscutal membrane.

Deutonymph: length 283 μ ; width 172 μ ; dorsal shield with 17 pairs of setae, arranged as in adult but longer in proportion to body. Seven pairs of setae surrounding anal plate in nymphs of both sexes. Sexes indistinguishable.

Adult Stages (Figs 24 and 26).

Female: length 345 μ ; width 221 μ ; dorsal chaetotaxy as in deutonymph, but setae shorter in proportion to body. Ventrianal shield present with three pairs of setae in addition to para-anals. A pair of pores present.

Male: length $261\ \mu$; width $144\ \mu$; dorsal chaetotaxy as in female except that S1 and S2 are on edge of shield instead of on interscutal membrane. Ventrianal shield present with six pairs of setae in addition to para-anals. Both sexes of this species were described by Chant (1956).

DISCUSSION.

The foregoing descriptions are brief, and give only characters of taxonomic value. Most of the gross characters as explained above, do not differ between species. Minor anatomical characters, such as those of the chelicerae, are of little value for practical identification though they may show differences between species. Generally, dentition of chelicerae is constant throughout development except in the adult male. However, variation may occur even within one stage and therefore these characters are of little use except perhaps to confirm dubious or difficult identifications. Only the chelicerae of common species were examined because, in doing so, specimens were usually destroyed.

The chaetotaxy of the legs is difficult to examine and is of little value to field workers. In most species, leg characters are similar but distinctive features are present in a few. In most larvae, the genu, tibia, and basi-tarsus of leg III have macrosetae that become progressively less differentiated in later stages and are absent in adults. Leg IV of the protonymph also has macrosetae that probably assume the function of those on larval leg III. Perhaps these extremely long setae, always most pronounced in immature stages, together with the long setae on the posterior dorsal shield and L4 in the larva and the relatively long setae of nymphs, have been evolved as protection from cannibalism and predation by adults of other phyto-seiid species. Cannibalism by adults is common in the family and usually takes the form of feeding on immature stages rather than on other adults. When a protruding seta of an immature mite is lightly touched, evasive action results. As the mites mature the need for such protection becomes progressively less, and the degree of setal specialization also decreases.

The complex of setae on tarsus I in larvae also seems of some taxonomic significance, though of little apparent practical value. This complex changes during development, as shown in the drawings of *T. bakeri*, and also differs between species.

Apart from minor chaetotactic variations in adults used for specific determination, there seem to be two broad types of setal pattern within the four genera studied. First, there is a simple type with only four anterior lateral setae on the "shoulder" of the adult dorsal shield, as in *Amblyseius*, *T. umbraticus*, *T. finlandicus*, *T. cucumeris*, and others; and second, a more complex type with five or more anterior lateral setae, as in *T. tiliae*, *T. rhenanus*, *T. bakeri*, *S. simplex*, *P. macropilis*, and others. The author considers that a more natural division between the genera *Amblyseius* and *Typhlodromus* might be established on this basis rather than on the character of relative setal length used up to now. In support of this each type is characterized by certain chaetotactic features of its immature stages. Dorsally, the simple type with only four anterior lateral setae is complete in the protonymph, in that no more setae are added. On the other hand, in the more complex type, seta L3 is absent in the protonymph, leaving a distinct gap between L2 and L4. This seta is added during the second moult and thus it is not until the deutonymph stage that the dorsal shield bears a full complement of setae. This seems to be a fundamental difference between the two types and no exceptions were found in the 18 species examined. Details are shown in Fig. 1.

This difference cannot be linked with any ventral character as protonymphs of all species have four pairs of setae around the anal plate in both sexes, except that *S. simplex* has three. In all species examined, male deutonymphs were present and each sex bore the same number of posterior ventral setae as the adults, though in the latter some of these setae are situated on the ventrianal shield. Sexual differences

are therefore lacking in protonymphs, except that in *T. finlandicus* the positions of the posterior ventral setae show sexual dimorphism. In deutonymphs, sexual differences are apparent except in those species of which both sexes of the adult have the same number of posterior ventral setae—i.e., *T. umbraticus* and *A. graminis*, in both forms of which seven pairs of setae are present.

On the basis of chaetotaxy, several types can be distinguished in the larvae of phytoseiids, but none are linked with adult characters. The number and positions of the setae on the anterior dorsal shield are constant, though relative lengths are of taxonomic value. The number of setae on the posterior shield, however, varies considerably. Basically, the long, whip-like setae are always present; these may be alone, or, as in *T. bakeri*, a second, minute, pair of setae may be present, also on the posterior margin of the shield. More commonly, one or two pairs of minute setae may be present on the anterior edge of the shield, as in *T. umbraticus* and *A. graminis*. Ventrally, either four or six pairs of setae may be associated with the anal plate; if there are only four the posteroventral pair are missing. Again, this is not linked with any adult character.

It is in larvae that the greatest differences between closely allied species are found. *T. reticulatus* and *T. cucumeris* were thought to be synonymous and yet their larvae differ considerably. Similarly, it is difficult to distinguish between adult females of *T. cucumeris* and *T. marinus* but again larval differences are striking. Finally, *T. aceri* and *T. tiliarum* show only minor adult differences, but in the larvae accurate separation can be based on the length of seta D4. Thus, a study of larval forms may help to solve systematic problems involving the adults.

A summary of these chaetotactic characters of the immature stages of the species studied is given in Table I. Keys for the identification of immature phytoseiids and for the adults of the species occurring in south-eastern England are given below. Nymphs of closely related species cannot be distinguished from one another, though in every case the larvae are distinct.

TABLE I.—Chaetotaxy of the Phytoseiidae in South-eastern England, showing the number of pairs of setae that surround the anus in both sexes, and the number of pairs of anterior lateral setae on the dorsal shield.

Species	Larva		Protonymph			Deutonymph			Adult		
	Both sexes		♂	♀	Both	♂	♀	Both	♂	♀	Both
					Ant. lateral			Ant. lateral			Ant. lateral
	Anal	Lateral	Anal	Anal		Anal	Anal		Anal	Anal	
<i>T. bakeri</i>	6	6	4	4	4	6	8	5	6	8	5
<i>T. tiliae</i>	4	5	4	4	4	6	8	5	6	8	5
<i>T. finlandicus</i>	4	5	4	4	4	4	7	4	4	7	4
<i>T. umbraticus</i>	6	7	4	4	4	7	7	4	7	7	4
<i>T. aberrans</i>	6	5	4	4	4	4	7	4	4	7	4
<i>T. rhenanus</i>	4	5	4	4	4	5	8	5	5	8	5
<i>T. reticulatus</i>	6	6	4	4	4	6	7	4	6	7	4
<i>T. soleiger</i>	4	5	4	4	4	3	6	5	3	6	5
<i>T. tiliarum</i>	6	6	4	4	5	6 ?	8	6	6	8	6
<i>T. masseei</i>	6	6	4	4	4	5 ?	7	4	5	7	4
<i>T. cucumeris</i>	4	6	4	4	4 ?	4 ?	7 ?	4	4	7	4
<i>T. marinus</i>	6	7	4	4	4	6	7	4	6	7	4
<i>T. aceri</i>	6	6	4	4	5	6	8	5	6	8	5
<i>P. macropilis</i>	6	5	4	4	4	4	6	5	4	6	5
<i>S. simplex</i>	6	5	3	3	5	5	7	6	5	7	6
<i>A. graminis</i>	6	6	4	4	4	7	7	4	7	7	4

KEY TO LARVAE OF PHYTOSEIIDAE.		
A ¹ .	Five pairs of lateral setae on dorsum	B
B ¹ .	Four pairs of setae surrounding anal plate	C
C ¹ .	A readily visible pair of pores associated with pre-anal setae	T. finlandicus
C ² .	Without such pores	D
D ¹ .	Setae D3, D4, and M1 extremely long	T. occidentalis
D ² .	Setae D3 and M1 of normal length	E
E ¹ .	Seta D4 short, less than L1 in length	T. tiliae
E ² .	Seta D4 longer than L1	F
F ¹ .	Seta D4 two to three times as long as L1	T. rhenanus
F ² .	Seta D4 approximately 10 times as long as L1	T. soleiger
B ² .	Six pairs of setae surrounding anal plate	C
C ¹ .	Seta D4 and posteroventral setae long	S. simplex
C ² .	Seta D4 and posteroventral setae short	D
D ¹ .	Seta D1 much shorter than L1, minute; L1 longer than L2 or L3	P. macropilis
D ² .	Seta D1 longer than L1; L1 and L2 equal in length	T. aberrans
A ² .	Six pairs of lateral setae on dorsum	B
B ¹ .	Four pairs of setae surrounding anal plate	T. cucumeris
B ² .	Six pairs of setae surrounding anal plate	C
C ¹ .	Seta L5 paired with L6, both on posterior margin of posterior dorsal shield	T. bakeri
C ² .	Seta L5 on anterior margin of posterior dorsal shield, not paired with L6	D
D ¹ .	Seta L2 equal in length to L3	T. masseei
D ² .	Seta L2 shorter than L3	E
E ¹ .	Seta L3 shorter than D1, para-anal setae short	T. reticulatus*
E ² .	Seta L3 equal to or longer than D1; if the former, para-anals long	F
F ¹ .	Seta L3 equal in length to D1, para-anals extending more than half their length beyond posterior margin of body	A. graminis
F ² .	Seta L3 longer than D1, para-anal setae short	G
G ¹ .	Seta D4 shorter than L3 or D1	T. aceri
G ² .	Seta D4 longer than L3 or D1	T. tiliarum
A ³ .	Seven pairs of lateral setae on dorsum	B
B ¹ .	Seta L1 equal to or longer than L3	C
C ¹ .	Seta D4 short	T. newsami
C ² .	Seta D4 long	T. marinus
B ² .	Seta L3 longer than L1	T. umbraticus

KEY TO PROTONYMPHS OF PHYTOSEIIDAE IN SOUTH-EASTERN ENGLAND.		
A ¹ .	Anterior lateral setae on dorsal shield smooth; S1 on interscutal membrane	B
B ¹ .	Eight pairs of lateral setae on dorsal shield	C
C ¹ .	Setae on dorsal shield short; a conspicuous gap between second and third lateral setae (i.e., L3 absent), eighth lateral seta and M2 paired	T. tiliae
C ² .	Setae on dorsal shield long, anterior four lateral setae equally spaced, eighth lateral seta, M2, and ninth lateral seta forming a triangle	T. aberrans
B ² .	Nine pairs of lateral setae on dorsal shield	C
C ¹ .	A conspicuous gap apparent between second and third lateral setae, setae short	D
D ¹ .	Three pairs of dorsal median (M) setae and a total of 18 pairs on dorsal shield	T. soleiger
D ² .	Two pairs of dorsal median setae and a total of 17 pairs on dorsal shield	E
E ¹ .	Very faint serrations on posterior setae on dorsal shield, macrosetae on leg IV with terminal knobs, movable digit of chelicera with two teeth; a bark-inhabiting species	T. bakeri

* Specimens of *T. reticulatus* occasionally have seven pairs of lateral setae on the dorsum. These key to *T. umbraticus* and can be distinguished from that species by the relative lengths of L1 and L2—in *T. umbraticus* L2 is equal to or longer than L1, whereas in *T. reticulatus* L2 is shorter than L1.

- E². Without serrations on posterior setae of dorsal shield, macrosetae on leg IV without terminal knobs, movable digit of chelicera with one tooth; mostly leaf-inhabiting species
T. rhenanus D
- C³. Without a gap between second and third anterior lateral setae on dorsal shield, setae as long as or longer than distances between their bases*A. graminis* E
- D¹. Setae L4, L9, and M2 moderately long and whip-like*T. finlandicus* F
- D². Setae L4, L9, and M2 not long and whip-like*T. masseei* G
- E¹. At least setae L1, L3, and L4 much longer than distances between their bases*T. umbraticus*
- F¹. A conspicuous pair of pores associated with pre-anal setae*T. reticulatus*, *T. cucumeris*, *T. marinus* C
- F². Without such pores*S. simplex* D
- G¹. Seta L2 less than half as long as L1*T. aceris*
- G². Seta L2 more than half as long as L1*T. tiliarum*
- E³. Setae L1, L2, and L4 only slightly longer than distances between their bases*P. macropilis*
- A². All lateral setae on dorsal shield strongly serrated, S1 on edge of dorsal shield

KEY TO FEMALE DEUTONYMPHS OF PHYTOSEIIDAE IN SOUTH-EASTERN ENGLAND.

- A¹. Lateral setae on dorsal shield smooth or only slightly serrated, S1 on interscutal membrane*B*
- B¹. Eight pairs of lateral setae on dorsal shield*T. aberrans* C
- B². Nine pairs of lateral setae on dorsal shield*T. tiliae* D
- C¹. Eight pairs of posterior ventral setae surrounding anal plate*A. graminis* E
- C². Seven pairs of setae surrounding anal plate*T. finlandicus* F
- D¹. Setae L4, L9, and M2 long and whip-like*T. umbraticus*
- D². Setae L4, L9, and M2 shorter, although still longer than remaining setae*T. masseei*
- E¹. A conspicuous pair of pores associated with pre-anal setae*T. reticulatus*, *T. cucumeris*, *T. marinus* C
- E². Without such pores*S. simplex* D
- F¹. Anterior lateral setae on dorsal shield longer than distances between their bases*T. aceris*
- G¹. Seta L1 approximately equal to L2 in length; dorsal shield less than 300 μ in length*T. tiliarum*
- G². Seta L1 longer than L2; dorsal shield more than 300 μ in length*T. bakeri*
- F². Anterior lateral setae on dorsal shield shorter than distances between their bases*T. rhenanus*
- B³. With 10 pairs of lateral setae on dorsal shield*T. soleiger* D
- C¹. With 19 pairs of setae on dorsal shield (three median pairs); six pairs of setae surrounding anal plate*T. bakeri*
- C². With 18 pairs of setae on dorsal shield (two median pairs); eight pairs of setae surrounding anal plate*T. rhenanus*
- D¹. Posterior setae on dorsal shield slightly serrated, one macroseta on leg IV, movable digit of chelicera with two teeth; bark-inhabiting*S. simplex* D
- D². Posterior setae on dorsal shield *usually* smooth, three long macrosetae on leg IV, movable digit of chelicera with one tooth; mostly leaf-inhabiting*T. tiliarum*
- B⁴. With 11 pairs of lateral setae on dorsal shield*T. soleiger* D
- C¹. Seven pairs of setae surrounding the anal plate*T. bakeri*
- C². Eight pairs of setae surrounding anal plate*T. rhenanus*
- D¹. Setae L9 and M2 paired, setae on dorsal shield short, three pairs of conspicuous pores on dorsal shield*T. tiliarum*

- D². Setae L9, L10, and M2 forming a triangle, without conspicuous pores on dorsal shield, setae on dorsal shield longer **T. aceri**
- A². All lateral setae on dorsal shield strongly serrated, S1 on edge of dorsal shield **P. macropilis**

KEY TO ADULT FEMALES OF PHYTOSEIIDAE IN SOUTH-EASTERN ENGLAND.

- A¹. Lateral setae on dorsal shield smooth or only slightly serrated, S1 on interscutal membrane **B**
- B¹. Eight pairs of lateral setae on dorsal shield **T. aberrans**
- B². Nine pairs of setae on dorsal shield **C**
- C¹. Setae L4, L9, and M2 long and whip-like **A. graminis**
- C². Setae L4, L9, and M2 less noticeably long, although they may be longer than others **D**
- D¹. Four pairs of setae on ventrianal shield **T. tiliae**
- D². Three pairs of setae on ventrianal shield **E**
- E¹. A conspicuous pair of pores associated with pre-anal setae on ventrianal shield, ventrianal shield oval in shape **T. finlandicus**
- E². Without such pores, ventrianal shield more nearly triangular in shape **F**
- F¹. Setae L1, L2, L3, and L4 much longer than the distances between their bases, dorsal shield greater than 400 μ in length **T. masseei**
- F². Setae L1, L2, L3, and L4 only slightly longer, or shorter than distances between their bases, dorsal shield less than 400 μ in length **G**
- G¹. Setae L1, L2, L3, and L4 only slightly longer than, or equal in length to, distances between their bases **T. umbraticus**
- G². Setae L1, L2, L3 and L4 shorter than distances between their bases **H**
- H¹. Ventrianal shield as broad as long **T. reticulatus**
- H². Ventrianal shield longer than broad **I**
- I¹. Setae L1, L2, and L3 less than half as long as distances between their bases **T. marinus**
- I². Setae L1, L2, L3 greater than half as long as distances between their bases **T. cucumeris**
- B³. With 10 pairs of lateral setae on dorsal shield **C**
- C¹. With 19 pairs of setae on dorsal shield (three median pairs), two pairs of setae on sole-shaped ventrianal shield **T. soleiger**
- C². With 18 pairs of setae on dorsal shield (two median pairs), four pairs of seta on triangular ventrianal shield **D**
- D¹. Anterior edge of ventrianal shield rounded, shield creased in lateral direction, one scarcely noticeable macroseta on leg IV **T. bakeri***
- D². Anterior edge of ventrianal shield nearly square, shield smooth, three large macrosetae on leg IV **T. rhenanus**
- B⁴. With 11 pairs of lateral setae on dorsal shield **C**
- C¹. Two pairs of setae on square ventrianal shield, setae on dorsal shield thick and thorn-like **S. simplex**
- C². Four pairs of setae on rectangular ventrianal shield, setae on dorsum normal **D**
- D¹. Ventrianal shield much longer than broad, seta M2 paired with L9, three pairs of conspicuous pores on dorsal shield **T. tiliarum**
- D². Ventrianal shield only slightly longer than broad, M2, L9, and L10 forming a triangle, no conspicuous pores on dorsal shield **T. aceri**
- A². Lateral setae on dorsal shield very long and serrated, S1 on edge of dorsal shield **P. macropilis**

* Nesbitt (1951) stated that these creases in the ventrianal shield are formed by the edges of one or more subsidiary plates on the shield. The present author considers that they are formed by the pressure exerted on the mite between the cover glass and the microscopic slide, which flattens the uniquely convex ventrianal shield and thus forms the creases or "wrinkles" apparent in Fig. 19b.

KEY TO ADULT MALES OF PHYTOSEIIDAE IN SOUTH-EASTERN ENGLAND.

- A¹. Lateral setae on dorsal shield smooth or only slightly serrated, S1 and S2 present B
 B¹. Eight pairs of lateral setae on dorsal shield *T. aberrans* C
 B². Nine pairs of lateral setae on dorsal shield C
 C¹. Setae L4, L9, and M2 long and whip-like *A. graminis* D
 C². Setae L4, L9, and M2 less noticeably long D
 D¹. Five pairs of setae on ventrianal shield E
 E¹. Five pairs of anterior lateral setae on dorsal shield, M2 paired with L8 *T. tiliiae*
 E². Four pairs of anterior lateral setae on dorsal shield, M2 paired with L7 or forming a triangle with L7 and L8 F
 F¹. Setae L1, L2, and L3 more than half as long as distances between their bases *T. reticulatus*
 F². Setae L1, L2, and L3 less than half as long as distances between their bases *T. marinus*
 D². Some other number than five pairs of setae on ventrianal shield E
 E¹. Six pairs of setae on ventrianal shield *T. umbraticus* F
 E². Less than six pairs of setae on ventrianal shield F
 F¹. Four pairs of setae on ventrianal shield *T. masseei** G
 F². Three pairs of setae on ventrianal shield G
 G¹. A pair of conspicuous pores associated with pre-anal setae *T. finlandicus*
 G². Without such pores *T. cucumeris* C
 B³. With 10 pairs of lateral setae on dorsal shield C
 C¹. Two pairs of setae on ventrianal shield *T. soleiger* D
 C². More than two pairs of setae on ventrianal shield D
 D¹. Four pairs of setae on ventrianal shield *T. rhenanus*
 D². Five pairs of setae on ventrianal shield *T. bakeri* C
 B⁴. With 11 pairs of lateral setae on dorsal shield C
 C¹. Four pairs of setae on ventrianal shield *S. simplex* D
 C². Five pairs of setae on ventrianal shield D
 D¹. Setae M2 and L9 paired, three pairs of conspicuous pores on dorsal shield *T. tiliarum*
 D². Setae M2, L9, and L10 forming a triangle, no conspicuous pores on dorsal shield *T. aceri*
 A². Lateral setae on dorsal shield greatly lengthened and serrated, S2 absent *P. macropilis*

* Not seen by the author.

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A CONTRIBUTION TO THE TAXONOMY OF SOME BRITISH SPECIES OF SAPPAPHIS MATSUMURA 1918 (HOMOPTERA, APHIDOIDEA).* By H. L. G. STROYAN, F.L.S., Ministry of Agriculture, Fisheries & Food, Plant Pathology Laboratory, Harpenden, Herts.

(With 2 Text figures).

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* Since the manuscript of this communication was submitted I have received a copy of a paper published in the Soviet Union (G. C. Shaposhnikov, 1956: The phylogenetic basis of a system of the Short-tailed Aphids (Anuraphidina) etc.; *Trudy Zoologicheskii Institut, Akademii Nauk S.S.S.R.*, 23, 215-320) which demonstrates from material in the author's possession that the Japanese genus *Sappaphis* Matsumura is not congeneric with the species discussed in the following pages. Henceforward the European species of aphids hitherto placed in *Sappaphis* will be placed in *Dysaphis* Börner, 1931. The complex of species treated in this paper will fall into *Dysaphis sensu stricto*, while the subgenus *Sappaphis* auct., *sensu stricto*, will be replaced by the subgenus *Pomaphis* Börner, 1939. The *typus generis* of *Dysaphis* is *Aphis angelicae* C. L. Koch, 1854, that of *Pomaphis* (originally erected as a genus) is *Aphis pyri* Boyer de Fonscolombe, 1841.
29 April 1957.

INTRODUCTION.

The British species of *Sappaphis* Matsumura fall into three rather well-defined groups, which may for convenience be designated subgenera. The typical subgenus *Sappaphis sensu stricto* comprises such species as *S. plantaginea* (Pass.), *S. pyri* (Fonse.), *S. sorbi* (Kltb.) and *S. aucupariae* (Buckt.) (Stroyan, 1957). The subgenus *Chomaphis* Mordvilko is confined monoeciously to tubuliflorous Compositae and contains only two western European species, both very rare in Britain, *S. lappae* (Koch) and *S. cirsii* (Börner). The subgenus *Dysaphis* Börner, with which this contribution deals, may be held to include all those species placed by Börner (1950, 1952) in *Yezabura* Matsumura and *Dysaphis* Börner. Of these species one group is associated with apple as primary host, a second group with hawthorn, while a few species have become secondarily monoecious on herbaceous hosts, with either a complete or incomplete cycle.

Until 1950 it was commonly recognized that two species of *Sappaphis* were concerned in producing galls on hawthorn in the spring. These were *S. crataegi* (Kltb.) and *S. ranunculi* (Kltb.). A personal communication to the writer by Dr. Hille Ris Lambers suggested that of these two, *S. crataegi* produced red galls and *S. ranunculi* yellowish ones. No indication of a satisfactory nature was to be found in literature regarding morphological discriminants between the two species. Hille Ris Lambers (1948), however, stated that *S. crataegi* may be "easily recognised [from the other European species] by its very short antennal hairs". He further quoted (l.c.) as secondary hosts *Daucus*, *Aethusa*, *Apium*, *Petroselinum* etc., and suggested as a synonym *Anuraphis apiifolia* Theob.

In 1950 Börner published a short conspectus of the genus *Yezabura* which he later (1952) repeated in catalogue form and amplified with statements about the biology of the species. From these accounts it became apparent that he recognized eight species and five subspecies of *Yezabura* as causative agents of galling on *Crataegus*. These were keyed in the manner following (Börner, 1950, translated by H. L. G. S.):

- 1 (7) All cephalic and dorsal hairs long
- 2 (3) Dorsal hairs long and finely produced apically; on *Heracleum* (and *Conium*)
lauberti Börner, 1940
- 3 (2) Dorsal hairs shorter and bluntly pointed.
- 4 (5, 6) Rostral length 0.4 to 0.6 mm.; on tulip tulipae B. de F., 1841
- 5 (4, 6) Rostral length 0.6 to 0.65 mm.; on *Laserpitium* laserpitii Börner, sp. nov.
- 6 (4, 5) Rostral length 0.65 to 0.83 mm.; on *Angelica* angelicae Koch, 1854
- 7 (1) Hairs on vertex (or all cephalic hairs) short.
- 8 (13) Longest hair of ant. III two-fifths to one-half diameter of joint or more; on
Ranunculus.
- 9 (10) Processus terminalis more than four times basal part of ant. VI, dorsum with all
segments banded, posterior spinal tubercles absent . . . annulata Börner, sp. nov.
- 10 (9) Processus terminalis at most three times base of VI, dorsum of middle body
segments unbanded, eighth, or seventh and eighth tergites, with spinal
tubercles.
- 11 (12) Longest frontal hairs two-thirds to three-quarters as long as the distance
between them; on *Ranunculus repens* ranunculi Kltb., 1843
- 12 (11) Longest frontal hairs up to half as long as the distance between them; on
Ranunculus bulbosus ranunculi ssp. bulbosi Börner, ssp. nov.
- 13 (8) Longest hair of ant. III one-quarter to one-third diameter of joint; posterior
abdominal segments usually with spinal tubercles; on Umbelliferae.
- 14 (15) Processus terminalis 0.33 to 0.39 mm. long; dorsum without wax powder;
on *Aethusa* aethusae Börner, sp. nov.
- 15 (14) Processus terminalis 0.17 to 0.32 mm. long; dorsum powdered.
- 16 (19) Frontal hairs of young larva distinctly longer than those on vertex; eighth
tergite in adult with long spinal hairs.
- 17 (18) Larval and nymphal fundatrigeniae pale green; summer host *Pastinaca*
kunzei Börner, sp. nov.

- 18 (17) Larval and nymphal fundatrigeniae reddish-tinged; summer host *Daucus crataegi* Kltb., 1843 (with biological subspecies on *Anthriscus* (*anthrisci* Börner, ssp. nov.) and *Aegopodium* (*aegopodii* Börner, ssp. nov.)).
- 19 (16) All cephalic hairs of young larva short; eighth tergite with short spinal hairs; body of adults less or not powdered; summer host celery. *inculta* Wlk., 1849 (= *apitfolii* Theob., *ferruginea-striata* Essig) (with biological subspecies on parsley (*petroselinii* Börner, ssp. nov.) and *Levisticum* (also *Conium*) (*nudicaulium* Börner, ssp. nov.)).

No information was given by Börner in 1950 on the experimental or other methods by which this picture was arrived at; but in the 1952 catalogue the words "Migr.-Test" were used, in conjunction with a name and date, e.g. "Börner 1931, Mordvilko, 1907" for each species to which a heteroecy was assigned. This was the sole information vouchsafed.

The publication of these papers raised a number of important questions concerning the British *Sappaphis* fauna. It appeared that two widely opposed views, which might roughly be called the "lumping" and "splitting" views, were current regarding the composition of the complex of forms forming galls on *Crataegus*. Neither of these views, however, was sufficiently well documented in the literature to offer firm ground for a critical appraisal. The views of both the principal protagonists—the late Dr. Carl Börner and Dr. Hille Ris Lambers—regarding the performance and significance of transference experiments were fairly well known to the writer; those of the former through perusal of his "Züchtung der Homopteren" (Börner in Abderhalden, 1926), and those of the latter through personal contact; but as neither had given any details of experiments performed with species of *Sappaphis* this was not in itself of any great assistance.

It was therefore necessary to attack the problem of the British hawthorn *Sappaphis*, if not quite *ab initio*, at least with an open mind; and a programme of work was undertaken designed to test as many as possible of the biological and morphological conclusions embodied in Börner's papers of 1950 and 1952. The account which follows is presented, not as a final elucidation of the problems arising in the taxonomy of the British *Sappaphis* living on *Crataegus*, but as a contribution towards their truer appreciation.

1. PRELIMINARY OBSERVATIONS.

During the years 1947–50 a fair quantity of material of *Sappaphis* was collected in the field, and the following were available for morphological study:

Fundatrices and spring migrants from both red and yellowish galls on *Crataegus*.
Apterous and alate viviparae from:

<i>Daucus carota</i>	<i>Conium maculatum</i>
<i>Pastinaca sativa</i>	<i>Petroselinum sativum</i>
<i>Aethusa cynapium</i>	<i>Angelica sylvestris</i>
<i>Torilis japonica</i> (<i>Caucalis anthriscus</i>)	<i>Ranunculus repens</i>
<i>Heracleum sphondylium</i>	<i>Smyrniolum olusatrum</i> .

In addition to this collection of material, some preliminary transference tests had been made using yellow-green galls from *Crataegus*, from which successful colonies had been obtained on *Ranunculus*; and using deep red galls from *Crataegus* from which successful colonies were obtained on cultivated carrot. These experiments were performed in the spring of 1949 and 1948 respectively. In the light of later developments it must appear that the successful result of the carrot transfer was due to chance rather than to accurate forecasting, since no other host than carrot was offered.

All this material was now examined critically in the light of Börner's key to *Yezabura* given above. The results, morphologically speaking, could not be fully

comparable with the key, since not all the forms keyed were available for study. However, some conclusions could be drawn. Taken species by species, these were as follows:

Sappaphis lauberti (Börner).—Long-haired forms agreeing with the original description (Börner, 1940) were recorded from leaf bases of *Heracleum*. Earliest finds were at the end of May, and consisted of single alatae with small numbers of progeny. This indicated heteroecy, but no comparable alatae were present in the available material from galls on hawthorn. The alatae had a very extensive and solid dorsal pigmented area on the abdomen, reaching almost or quite to the marginal sclerites; they only rarely showed paired or unpaired marginal tubercles on the seventh abdominal segment, and also rarely had any secondary rhinaria on ant. V.

S. angelicae (Koch).—Long-haired forms referable to this species were recorded from leaf bases of *Angelica sylvestris*. Early summer samples were not forthcoming, and no assumption could therefore be made about heteroecy. Available spring gall material contained no alatae similar to those from the summer host. These had a fairly extensive dorsal abdominal patch, only exceptionally an asymmetrical marginal tubercle on abd. 7, but apparently always bore a number of secondary rhinaria on ant. V.

S. ranunculi (Kltb.).—This species was apparently marked off from the others by a number of characters. First, the preliminary transfers had shown that alatae from yellow-green galls colonized *Ranunculus* but not *Daucus*. The aphids contained in these yellow-green galls were also different from those in the deep red ones. The fundatrices were larger, slate-grey or blue-grey in life, dark blackish-green when denuded in alcohol, and apparently did not bear spinal tubercles on the eighth abdominal tergite. Their progeny similarly were of a pure deep grey hue with a fine, even wax bloom, and produced rather large alatae which apparently always bore some secondary rhinaria on the fifth antennal joint. The progeny resulting from transference to *Ranunculus*, and also those apterae collected in the field on *Ranunculus*, contained a very large proportion of specimens with heavy abdominal pigmentation, either as segmental bands or in solid patches. These specimens, which predominated in the early generations on *Ranunculus*, were apparently a very constant type of alatiform, and usually also exhibited lengthening and darkening of the antennae together with the presence of a few secondary rhinaria scattered along joints III and IV. This type of alatiform aptera was not found in any of the other species under consideration, in which also the colour of the gall generations was never of a pure deep grey, but always greenish or pinkish tinged, while the rather smaller fundatrices were of a mottled grey-green when denuded, and usually showed one or two spinal tubercles on the eighth abdominal segment. The length of the body and antennal hairs also varied greatly in *ranunculi*. An examination of frontal hair lengths in samples taken from *Ranunculus repens* and *R. bulbosus* (2 collections) showed that in the aphids from *R. bulbosus* the longest frontal hairs varied from about two-thirds as long to nearly one and a half times as long as the distance between their bases. The range in most samples of aphids from *R. repens* was about the same, but two collections, one from Guernsey and one from the Netherlands, had a frontal hair length maximum of not more than one-third of the distance between their bases.

S. aethusae (Börner).—Forms with short antennal and dorsal hairs were collected on various occasions from *Aethusa cynapium*. These appeared indistinguishable from *crataegi* Kltb. on *Daucus*, except that the apterae had on the average a slightly longer processus terminalis. An apparently similar form was collected on one or two occasions from *Torilis japonica*. *Aethusa* being an annual weed associated with cultivated ground it appeared highly probable that heteroecy must occur. Comparison of the length of the processus terminalis for apterae of this and the two following forms (*kunzei* and *crataegi*) showed that in spite of the slightly higher average value of the ratio Processus terminalis/Basal part of VI in *aethusae*, the actual ranges of

absolute length of the processus in all three forms were almost identical (Stroyan, 1955). Marginal tubercles on the seventh abdominal segment in *aethusae* were rarely present, and alatae of the midsummer generation were nearly always without secondary rhinaria on ant. V.

S. kunzei (Börner).—Short-haired forms on *Pastinaca sativa* were collected in various localities in Cambridgeshire and West Suffolk. Apterae again appeared indistinguishable from those of *crataegi* Kltb. on *Daucus*. Alatae appeared to be characterized by a tendency to show lines of weakness intersegmentally in the mid-dorsal abdominal black patch. Secondary rhinaria on ant. V in alatae were exceptional, and marginal tubercles on the seventh abdominal segment of rare occurrence in both apterae and alatae. Alate males and gynoparae were bred from *Pastinaca* in September 1950.

S. crataegi (Kltb.).—Under this heading had hitherto been placed all aphids derived from deep red galls on hawthorn. These were distinguished from the gall generations of *S. ranunculi* by the colour and size differences noted under the latter species, and by the rather regular development of spinal tubercles on the posterior abdominal segments of the fundatrices. It was realized that the alatae falling into this category were not homogeneous, but it appeared impracticable to separate them into different species morphologically without a more careful investigation. The summer generations on *Daucus carota* (wild form) are apparently rare in the field round Cambridge. Such material as was available was not sufficient to give any very reliable discriminant for separation from *kunzei* and *aethusae*. Material from *Aegopodium* and *Anthriscus* (subspecies *aegopodii* and *anthrisci* Börner) were not collected at any time, but one sample taken on *Anthriscus* in Berkshire by Dr. V. F. Eastop, and consisting solely of apterae, did not differ in any obvious way from *crataegi* except by rather small size.

S. inculta (Wlk.) Börner.—Aphids collected from garden parsley in the summer appeared to be distinct from *crataegi*, *kunzei* and *aethusae* in several characters. The marginal tubercles were rather large and flat, and occurred with considerable regularity on the seventh abdominal segment; the hairs on the frons and the eighth tergite were very much shorter; and the alatae possessed a number of secondary rhinaria on ant. V, and a tendency for the mid-dorsal patch to be broken and narrowed anteriorly. Material agreeing with these characters was also found on *Smyrniolum olusatrum* in the Isle of Thanet in 1950. Certain alatae from red galls on hawthorn appeared to share the same characters, but the identity could not at the time be regarded as certain.

It will be seen that these preliminary observations, fragmentary as they were, had yet demonstrated that Börner's key of 1950 was incorrect in two particulars. First, the morphological distinction given for *S. ranunculi* (Kltb.) and its subspecies *bulbosi* Börner had proved invalid when applied to wild-collected aphids; and secondly, the criterion for separation of *S. aethusae* (Börner) from *S. kunzei* (Börner) and *S. crataegi* (Kltb.) had proved to be unreal. Forms not covered by the initial survey included one (*laserpitii* Börner) whose secondary host is not a British plant, and *S. tulipae* (B. de F.), for whose holocycle there is no evidence which bears examination (Theobald (1927) records finding a male, but the specimen concerned is a male of *S. plantaginea* (Pass.)). The characters of *S. annulata* (Börner) suggest that this may be based on extreme alatiform examples of *S. ranunculi* (Kltb.), in which the processus terminalis would probably be abnormally long and the banding of the abdomen very heavy. One of Börner's specimens shown to me by Dr. Hille Ris Lambers only differed inconsiderably from the most extreme forms of *ranunculi* in my possession.

2. AIMS OF THE EXPERIMENTAL PROGRAMME.

Questions left unresolved by the preliminary investigation might be summarized as follows :

(1) Could the various more or less morphologically recognizable species, i.e. *lauberti*, *angelicae* and *inculta*, which were not yet known from *Crataegus* galls, be traced to *Crataegus*?

(2) Was *ranunculi* the only species causing pale yellowish galls on *Crataegus*?

(3) Were the short haired forms *crataegi*, *kunzei* and *aethusae* really valid biological units with mutually exclusive host relations in the summer?

Plans for experimental work to resolve these outstanding questions were based on two premises. These were:

(1) That, once colonizations of *Heracleum*, *Angelica* and *Petroselinum* (or *Apium*) were obtained, it would be possible to dispense with further work on *S. lauberti*, *angelicae* and *inculta* and concentrate on the remaining species of the *crataegi* complex proper.

(2) That the facilities ideally necessary for a complete investigation of large numbers of galls would not be attainable.

Both these premises were to a great extent confirmed in the event.

3. LIMITATIONS IMPOSED BY AVAILABLE FACILITIES.

The conditions required in theory for a reliable choice test with spring alatae are as follows:

(1) Only freshly moulted spring migrant alatae should be used.

(2) The alatae used should be a pure sample (i.e. the progeny of one fundatrix).

(3) The alatae should be offered a choice of the various hosts to be tested, offered to them simultaneously, each plant species being in its natural growth phase and in normal physiological condition (i.e. without concealed wilting).

(4) The choice cage or chamber should permit an adequate amount of flight activity by the alatae prior to settlement.

(5) Evaluation of results should take account of the normal habits of the aphids tested (i.e. a species which normally lives basally should take up a basal position on the selected host in choice tests, and the progeny should maintain this habit and not disperse over the plant).

In order to comply with all the conditions enumerated above, it would be necessary to provide the alatae produced from each separate gall collected, with a full choice range of secondary hosts, all grown under natural conditions. The cages necessary to hold such a selection of hosts would need to be large enough to hold up to about eight potted plants apiece. The testing of each gall might therefore be said to require ideally from six to eight potted plants and a cage of perhaps 3 ft. \times 3 ft. \times 3 ft. cubic capacity. The large number of galls which it was proposed to test made this a quite unrealistic proposition initially; and it was decided to begin by testing the galls in batches until the elimination of certain species might permit a more refined procedure.

The provision of secondary hosts for presentation to the aphids was also a matter in which some limitations had to be recognized. The space and time available would not permit the simultaneous maintenance of more than about 100 to 120 pot-cultured plants altogether; and since it was obviously impossible to reproduce in culture the varying ecological niches occupied by the various plant species it was decided from the outset to accept an artificial uniformity of growth conditions by growing all plants, whether from seed or collected in the field, in a uniform compost.

A further ecological factor which it was decided to eliminate from the tests was the ministrations of attendant ants. It was felt that providing and isolating an ant colony for each plant would complicate matters to a degree not at all likely to be compensated for by the possibly beneficial effect of the association to the settled aphids, especially since the initial host choice of the aphids was to be influenced as little as possible by any factors other than the properties of the hosts offered.

These various limitations of the method to be used were expected to influence the results of the experiments in the following ways:

(1) By presenting the plants for choice to large batches of pooled alatae from different galls the concentration of alatae in the cages would be raised far above that prevailing in the field, even in the immediate vicinity of primary host trees. This, and the restraint placed upon dispersal by the limitations of the cages used, would probably cause some amount of abnormal behavioural reactions between individual aphids. Aggregation behaviour is a marked feature of many alate aphids when settling on a host, and under these conditions might well produce some settlement on inappropriate hosts in an assemblage consisting of more than one species or subspecies of aphid.

(2) By presenting host plants grown under uniform conditions of nutrition, illumination and water supply in an unnatural juxtaposition one is in effect reducing the quantity of critical sense data presented to the individual aphid in the selection of its host. This must necessarily reduce the insect's host-selecting efficiency.

The bias introduced by these factors would be expected to result in an apparent lowering of host-specificity among the members of the complex to be studied. It therefore follows that, while any positive evidence of such specificity obtained from the tests could be given full weight in assessing the results, negative evidence should be treated with reserve pending confirmation under more stringent conditions. This should be particularly borne in mind in considering the data recorded hereafter.

Cross-transference from one secondary host to another was ruled out of the experimental programme as a means of testing biological isolation, since it was anticipated that the effect of conditioning to the first host selected would render the accuracy of the results suspect, and since the inaccuracies produced would be of the opposite tendency to those of the main experiments : i.e. they would tend to produce a spurious host specificity even in cases where no genuine specificity existed. This opposite tendency when placed against the tendency of the experimental conditions to damp down specificity would render it impossible to regard with confidence any evidence obtained, whichever way it might incline.

4. METHODS EMPLOYED.

Rearing of Plants.

(a) Seed was sown in late February in standard John Innes compost in size 16 flowerpots. Seedlings raised from this seed were used to follow on and supplement

(b) plants collected in March by digging up in the rosette stage, and potted up in John Innes compost.

Collection of Aphid Material (1951).

Galls were collected from *Crataegus* at a time when the contained nymphs were in their final instar. Each gall was placed in a separate 3 in. \times 1 in. glass tube, plugged with cotton wool and accompanied by a small corymb of unopened flower buds, on the pedicels of which the nymphs were found to feed satisfactorily if and when the gall became unsuitable through desiccation. Each gall was given a reference number consisting of a prefix letter and a numeral between 1 and 10 inclusive. So far as possible a complete set of ten galls was collected from each bush or tree infested, and the ten were selected if possible for homogeneity of coloration.

On emergence of the alatae from the galls a random sample of up to three specimens was drawn from each gall initially (random except in so far as this sample was usually drawn from among the earlier emergences), and preserved for subsequent examination. If a gall later produced more alatae than were deemed necessary for the actual transference test, the surplus was added to the initial gall sample. The rest of the alatae were pooled in each batch of 10 samples (i.e. all series A together, etc.), and used for transference.

Method of Release (1951).

A group of plants to be offered as hosts was assembled under a cage of dimensions 3 ft. \times 2 ft. 6 in. \times 3 ft., consisting of muslin stretched over a wooden frame. The muslin was glued to the frames carefully all round to give an insect-tight construction. All plants were thoroughly watered immediately before the transference of alatae. A pooled batch of alatae from ten galls was then released into each cage. A period of 48 hours was then allowed for flight activity and settlement, after which the plants offered were examined for colonization, those with settled alatae being sleeved off under individual muslin cylinders.

In a number of cases, where whole batches of ten galls could not be collected from a single tree, or where batches of ten galls were obviously heterogenous, or single galls on preliminary examination agreed very markedly with the characters expected of a particular species, individual tests were performed with single galls or with groups of two or three, either a single host or a choice being offered according to the available cage space or the expected identity of the aphids. Such tests were obviously not designed to give coverage of all the possibilities, and were used merely so that the maximum amount of miscellaneous information, whether positive or negative, should be got from the series of experiments as a whole.

Recovery of Alatae.

After a lapse of a few days to enable the settled alatae to stock the selected plants with young progeny the colonized plants were re-examined, and the alatae removed and transferred to lactic acid and alcohol for morphological comparison with the original gall samples.

Breeding on of Colonies.

The colonies established were now bred on for as long as proved possible, and samples taken from them in each succeeding generation, so far as it was possible to distinguish generations after the F.I. In fact circumstances usually rendered it impossible to rear more than two generations on the secondary host, since the high concentration of aphids resulting from unchecked multiplication and the large number of alatae settling on each plant very speedily exhausted the plants and brought about the decline of the aphid colonies; while the number of plants which could be maintained made it impossible to start an adequate number of subcultures from the original colonies.

Examination of Material.

A selection of characters to be examined was made on the basis of the preliminary field observations and of the diagnoses contained in Börner's key of 1950.

Initial data recorded from the gall samples immediately after collection were:

(a) The colour of the galled leaf tissue. This was estimated on an arbitrary scale of scoring from 0 (pure greenish-yellow) to 5 (deep purplish-red).

(b) The live colour of the contained nymphs. This was judged in the presence of the wax pulverulence, not after denudation in alcohol.

(c) The degree of wax pulverulence of the nymphs. This was recorded on an arbitrary scale from 1 (almost nude) to 5 (heavily mealy).

Characters chosen for examination in the preserved alatae were:

(d) Body length.

(e) Length ratios of joints of the antennal flagellum (III-VI).

(f) Number of hairs on eighth abdominal tergite, and whether long (L) or short (S). intermediate lengths were recorded as long medium ([L]) or short medium ([S]).

(g) Length of longest measurable hair on third antennal joint.

(h) Length of longest measurable hair on second or third abdominal tergite.

(i) Presence or absence (2, 1 or 0) of marginal tubercles on seventh abdominal segment.

(j) Shape of abdominal marginal tubercles. This was expressed on an arbitrary scale from 1 (almost flat) to 4 (strongly protruding, subacute).

(k) Number of secondary rhinaria on fifth antennal joint.

(l) Size, shape and solidity of pigmented abdominal patch on the dorsum (hereafter referred to as the *macula*).

These characters, it was hoped, would have applications in determining the identity of species as follows :

(a) Separation of *ranunculi* from other members of the group.

(b) Separation of *kunzei* from *crataegi* (Börner, 1950).

(c) Separation of *aethusae* and *inculta* from other species.

(f) Separation of *inculta* from *crataegi*, *kunzei* and *aethusae*.

(g) and (h) Separation of *lauberti* and *angelicae* from the other species of the group (Börner, 1940, 1950).

(i) Not capable of identifying individuals, but useful in samples of several specimens for indicating the likelihood of the species being *inculta*.

(j) Separation of *inculta* from other species.

(k) Separation of *inculta*, *angelicae* and *ranunculi* from the rest of the group.

(l) Separation of *inculta*, *lauberti*, *kunzei* and *aethusae*.

It was anticipated that the combination of these characters would make it possible, in cases where the batch of alatae used in transference subsequently proved to be non-homogeneous, to identify fairly reliably the gall or galls from which the colonists of any given host were derived. This proved true within limits, although lack of certainty about the parentage of colonists was one of the inevitable weaknesses of the "pooled gall" method.

5. SUMMARY OF RESULTS (1951).

The results of the 1951 series of experiments may be summarized under three headings :

(i) The data recorded for each gall series before transference, and the host choice offered and accepted or rejected.

(ii) The data recorded from the morphological examination of recovered alatae from various hosts, compared with expectation based on preliminary observations and field collections..

(iii) Identifications of initial gall samples on purely morphological grounds, compared with colonizations actually recorded from the appropriate gall series.

5 (i). Gall Data.

The following abbreviations and classifications are used :

<i>Host plants.</i>	He	<i>Heracleum sphondylium</i> L.
	Pa	<i>Pastinaca sativa</i> L.
	Pe	<i>Petroselinum crispum</i> (Mill.) Airy-Shaw.
	Da	<i>Daucus carota</i> L.
	Ae	<i>Aethusa cynapium</i> L.
	An	<i>Anthriscus sylvestris</i> (L.) Bernh.
	Ang	<i>Angelica sylvestris</i> L.
	Ch	<i>Choerophyllum temulum</i> L.
	Sm	<i>Smyrniolum olusatrum</i> L.
	Ru	<i>Rumex obtusifolius</i> L.
	Ra	<i>Ranunculus repens</i> L.

Gall colour.	0	Pure greenish-yellow.
	1	Greenish-yellow tinged with pink in centre of galled area.
	2	Greenish-yellow, central part of galled area rosy-pink to rosy-red.
	3	Rosy-pink, edges of galled area yellow shading into the green of the leaf.
	4	Rosy-red, sharply demarcated at edges with no yellow tinge.
	5	Deep purplish-red, sharply demarcated at edges as in 4.
Wax powdering.	1	Very little bloom, body shiny through bloom.
	2	Slight but even bloom, general effect matt.
	3	Even fine coating, lending a greyish tinge to underlying colour of body.
	4	Somewhat coarser and heavier than 3, but not mealy.
	5	Rather heavy, coarsely granular or mealy, underlying colour hardly showing.

The following tables (see p. 654) show the recorded data for the gall samples collected in 1951, together with the hosts offered and the results obtained. The symbol + represents a successful colonization, the symbol — a negative result, and the symbol (+) a reluctant colonization with few or slowly developing progeny. The O.S. grid references given for the sites where galls were collected refer to Sheet 135 of the one-inch Ordnance Survey series (Cambridge and Ely).

5 (ii). *Data from Alatae Recovered from Secondary
Hosts after Colonization.*

(a) Recoveries from *Heracleum*.

Gall series A. Only 1 alata recovered. This was short haired on ant. III and abd. 2/3 (hair length 12μ), and with long acute hairs on abd. 8 (this combination will hereafter be referred to as S.S.L.); a pair of marginal tubercles were present on abd. 7 (this will hereafter be referred to as M.T./7:2); secondary rhinaria on ant. V (hereafter referred to as Rhin./V) 1 and 1. No colonization resulted, and this recovery was not in agreement with expectation.

Gall series E. 6 alatae recovered. Of these 2 were long haired on ant. III and abd. 2/3 (hair length $25-29\mu$ and $43-46\mu$ respectively) (this combination will hereafter be referred to as L.L.L.); M.T./7:0; mean Rhin./V (4 antennae) 1.25; dorsal macula very solid and extensive. The other 4 were of S.S.L. type; M.T./7:0; mean Rhin./V (8 antennae) 0.375; dorsal macula moderately extensive and solid. The 2 long-haired specimens agreed with expectation for *S. lauberti*. The F.1 progeny were sampled on 19.vi.51; all these apterae were long-haired. No short-haired progeny developed.

Gall series F. Two tests were performed with this series. In the first, where the aphids used were combined with those from galls N.1 and N.2, 11 alatae were recovered from *Heracleum*. All were of L.L.L. type; M.T./7:2 in one specimen, 1 in four, 0 in six; mean Rhin./V (22 antennae) 0.73. In the second test, using alatae from F only, 6 alatae were recovered from *Heracleum*. These also were all of L.L.L. type; M.T./7:1 in five, 0 in one; mean Rhin./V (12 antennae) 0.83. Apterous progeny from the second test were sampled on 19.vi.51. All were long haired. The dorsal macula in the recovered alatae was large and solid in those from the first test, slightly less so in the smaller specimens recovered from the second test. Agreement with expected characters of *lauberti* was 100 per cent in this test, apart from the rather high incidence of marginal tubercles on abd. 7.

Gall series G. Alatae from G.5, 8 and 10 were offered only *Heracleum*. No recoveries were made from this test, but ultimately a sparse culture developed and was maintained until the end of July. Hair lengths in samples drawn from this

TABLE I.—Gall sample data and choice tests (1951).

Gall series	Locality	O.S. grid ref.	Gall colour	Nymph colour	Wax powdering	Host choice									
						He	Pa	Pe	Da	Ae	An	Ang	Ch	Sm	Ru
A	Cambridge	436596	5	Pinkish	Not recorded	—	—	—	+	+	—	—	—	—	(+)
B	"	444586	0-2	Pure grey	3	—	—	—	—	—	—	—	—	—	—
C	"	443586	2-5	Pure grey to pinkish	2-3	—	—	—	—	—	—	—	—	—	—
D	"	446574	0-2	Pure grey	2-3	—	—	—	—	—	—	—	—	—	—
E	"	452573	2-5	Dove grey to pinkish	2-4	—	—	—	—	—	—	—	—	—	—
F (1st test with N)	"	454571	5	Pinkish	Not recorded	—	—	—	—	—	—	—	—	—	—
F (2nd test)	"	454571	5	"	Ditto	—	—	—	—	—	—	—	—	—	—
G.1	"	454571	4	Greenish	2	—	—	—	—	—	—	—	—	—	—
G.5, 8, 10	"	454571	2-5	Pinkish-grey to pinkish	3-5	—	—	—	—	—	—	—	—	—	—
H.1-4	Great Wilbraham	539574	0-2	Pure grey	3	—	—	—	—	—	—	—	—	—	—
H.5-8	"	537577	4-5	Pinkish	3	—	—	—	—	—	—	—	—	—	—
H.9-10	Little Wilbraham	547587	5	"	3	—	—	—	—	—	—	—	—	—	—
I.1	Wicken Fen	561709	3	Pure grey	3	—	—	—	—	—	—	—	—	—	—
I.2-10	"	562706	1-5	Pure grey to pinkish	3-5	—	—	—	—	—	—	—	—	—	—
K.1	Fulbourn	532569	2	Pure grey	3	—	—	—	—	—	—	—	—	—	—
K.2	"	532568	4	Lilac-grey	3	—	—	—	—	—	—	—	—	—	—
K.3	Cambridge	435595	5	Pinkish	3	—	—	—	—	—	—	—	—	—	—
K.4	Little Wilbraham	549583	4	"	3	—	—	—	—	—	—	—	—	—	—
M.1-3	Fulbourn	532569	3-4	Pure grey to pinkish	3	—	—	—	—	—	—	—	—	—	—
M.4, 6, 8, 9	Great Wilbraham	551574	5	Pinkish to pink	3	—	—	—	—	—	—	—	—	—	—
M.5, 7, 10	"	551574	5	Green	2-3	—	—	—	—	—	—	—	—	—	—
N.1-2 (with F)	Cambridge	454571	5	Pinkish grey	3	—	—	—	—	—	—	—	—	—	—

For choice data see under F (1st test)

culture were rather intermediate between the normal *lauberti* range (25–40 μ) and the normal *crataegi* range (9–14 μ). Some alatae bred out in July (midsummer generation) were similarly intermediate, had no secondary rhinaria on V and a single marginal tubercle on abd. 7 in only one out of five specimens. The characters of this material indicated that it was derived from gall G.8 only.

Gall series I. 12 recoveries. All of L.L.L. type. M.T./7: 1 in two, 0 in ten. 2 alatae had rather numerous rhinaria on 7 (mean Rhin./V for four antennae 9.75); the remainder had 0–3 only (mean Rhin./V for 20 antennae 0.35). These latter when of normal size had the macula solid and extensive, and agreed with the expected characters of *lauberti*; the former 2 agreed with expectation for *angelicae*. Agreement with expectation among the initial colonists was therefore 83 per cent. The F.1 was sampled on 19.vi.51. All were long haired, with M.T./7: 1 in two, 0 in 13.

Gall K.3. Predicted as *lauberti* from morphology of alatae (see 5 (iii)). Offered *Heracleum* only. Colonized successfully. 39 alatae recovered. All agree with gall sample, and are typical *lauberti* except for an abnormally high Rhin./V value (mean for 75 antennae 1.95). M.T./7: 1 in six, 0 in 33. Apterous progeny sampled in June and July were all long haired, with M.T./7: 1 in one, 0 in nine. Alatae were bred in the F.2 generation; a sample of five had mean Rhin./V (ten antennae) 1.60, and M.T./7: 1 in one, 0 in four.

Gall K4 (see 5 (iii)). 6 recoveries. All L.L.L. or with antennal and abdominal hairs rather long (a few comparable with gall G.8). M.T./7: 1 in one, 0 in five. Mean Rhin./V (12 antennae) 0.17. Macula extensive and solid. Progeny sampled in June and July agree in hair length with original alatae (ant. III 14–26 μ , abd. 2/3 18–50 μ), and have M.T./7: 1 in three, 0 in 21.

(b) Recoveries from *Angelica*.

Gall series I. 20 recoveries. Of these 13 combine L.L.L. chaetotaxy with a high Rhin./V count (2–17, mean of 26 antennae 8.50). These agree with the expected characters of *angelicae*. Three combine L.L.L. chaetotaxy with low Rhin./V counts (0–3, mean of six antennae 1.00). Four show S.S.L. chaetotaxy with Rhin./V count 0–6 (mean of eight antennae 1.50). The *angelicae* alatae have M.T./7: 2 in one, 1 in two, 0 in ten. Agreement with expectation among the initial colonists was thus 65 per cent. Progeny sampled in June and July were all long haired. M.T./7 data for progeny were: apterae 1 in three, 0 in 17, alatae 1 in three, 0 in seven. Rhin./V counts in alate progeny were 1–13 (mean of 20 antennae 3.50).

(c) Recoveries from *Petroselinum*.

Gall series E. 1 alata recovered. Chaetotaxy S.S.S. M.T./7: 0. Rhin./V 3 and 6. Agreed in general with expectation for *inculta*. Progeny gave rise to a small but healthy colony which was sampled in June and twice in July (5.vii.51 and 12.vii.51); all were of S.S.S. type (hairs on abd. 8 maximally 16–25 μ long). M.T./7 for progeny: 2 in seven, 1 in seven, 0 in three. These observations also agreed with expectation.

Gall G.1. Predicted as *inculta* from morphology (see 5 (iii)). Only *Petroselinum* offered. 1 recovery. Chaetotaxy S.S.S. M.T./7: 1. Rhin./V 1 and 5. Macula narrowing anteriorly as observed in wild *inculta*. Progeny sparse, five only recovered in June and July. All had S.S.S. chaetotaxy (hair length maxima on abd. 8 14–20 μ). M.T./7 for progeny: 2 in one, 1 in four. Agreed with expectation.

(d) Recoveries from *Pastinaca*.

Gall series C. 3 recoveries. 2 with chaetotaxy S.S.S. These had M.T./7 paired in both cases, and Rhin./V counts 3–9 (mean for four antennae 6.00). They agreed with *inculta* in morphology. The third had chaetotaxy S.S.L., M.T./7 absent and Rhin./V 0 and 4; the macula showed some weakness intersegmentally. This

specimen might have agreed with the expected characters of *kunzei*, but no progeny resulted, and no further conclusions could be drawn. Test negative.

Gall series H. 2 recoveries. Both with chaetotaxy S.S.L. Macula very extensive and solid. M.T./7 : 2 in one, 0 in one. Rhin./V 0-2 (mean 0.50). No progeny resulted. Test negative.

Gall K.2. Predicted as *kunzei* from morphology (see 5 (iii)). Offered *Pastinaca* only. 23 recoveries. All S.S.L. or S.S.[L]. haired. M.T./7 : 1 in four, 0 in 19. Rhin./V 0-3 (mean of 45 antennae 0.33). Macula variable, from nearly solid to much broken intersegmentally, the latter to some extent correlated with small size. Progeny sampled in June and July agreed in morphology with the original colonists, i.e. chaetotaxy S.S.L., Rhin./V (alatae) 0-1 (mean of 16 antennae 0.06), M.T./7 (alatae) : 1 in one, 0 in seven, (apterae) 1 in three, 0 in five.

Gall series M. (3, 4, 6, 8 and 9 only). 16 recoveries. All S.S.L. or S.S.[L]. Macula solid or nearly so in ten specimens, with more or less distinct intersegmental weaknesses in six. The former had M.T./7 : 2 in one, 1 in one, 0 in eight ; Rhin./V 0-4 (mean of 19 antennae 0.84). The latter had M.T./7 : 1 in two, 0 in four ; Rhin./V 0-4 (mean of 12 antennae 0.83). The resulting colony was weak, the plant being unhealthy. 5 apterae were recovered on 2.vii.51. Their chaetotaxy was as in the original colonists ; M.T./7 were paired in one, single in one, absent in three. Agreement with expectation of the original colonists was 37.5 per cent.

Gall series E. No recoveries. A sparse culture developed which was sampled on 19.vi.51. Six apterae were all of S.S.L. type, and without M.T./7.

Gall series I. No recoveries. A culture of apterae developed which was sampled on 18.vi.51 and 5.vii.51. All were of L.L.L. type (ant. III 45-61 μ , abd. 2/3 45-62 μ). M.T./7 : 1 in two, 0 in 11. Six alatae recovered in the July sample had M.T./7 : 1 in two, 0 in four ; Rhin./V 0. This sample agreed with the expected characters of *lauberti*.

(e) Recoveries from *Aethusa*.

Gall series A. 2 recoveries. Both S.S.L. haired. Macula extensive, solid. M.T./7 : 1 in one, 0 in one. Rhin./V 0-2 (mean of four antennae 0.75). F.1 progeny sampled 18.vi.51. These agreed in hair length with the original colonists. Single M.T./7 were present in two out of eight examined.

Gall series C. 3 recoveries. All S.S.S. haired. Macula somewhat broken. M.T./7 : 2 in two, 1 in one. Rhin./V 3-8 (mean of five antennae 6.00). Colonization failed. This result was in accordance with expectation, which was that alatae of this type should be *inculta*. Test negative.

Gall series E. 32 recoveries. 29 of these had chaetotaxy S.S.L. 3 had the antennal and abdominal hairs rather intermediate between long and short. Macula solid and extensive in all specimens except four where slight traces of weakness were present. M.T./7 : 2 in one, 1 in nine, 0 in 22. Rhin./V 0-3 (mean of 63 antennae 0.29). The resulting colony was very strong by mid-June, and was sampled first on 18.vi.51. All apterous progeny were S.S.L. haired ; M.T./7 data were : 2 in two, 1 in 17, 0 in 43.

Gall series F (1st test) and N. 40 recoveries, of which 38 were of S.S.L. type, one L.L.L. and 1 with intermediate hairs on antennae and abd. 2/3 (22 μ and 27 μ respectively). Macula extensive and solid, or nearly so, in all but one specimen. M.T./7 distribution for S.S.L. specimens : 2 in two, 1 in 17, 0 in 19. Rhin./V (S.S.L.) 0-5 (mean of 71 antennae 0.57). Progeny were sampled on 25.vi.51 (3 only) and 5.vii.51 (8 only). The June sample consisted of two S.S.L. and one L.L.L., the July sample of five S.S.L. and three L.L.L. apterae. The S.S.L. progeny had M.T./7 : 1 in one, 0 in six. Agreement with expectation for the original colonists based on hair length was 95 per cent.

Gall series F (2nd test). 14 recoveries. All S.S.L. except one, an S.S.S. alata of unknown origin, whose characters agreed in general with those of *inculta*. Ignoring this apparent intruder, agreement with expectation based on hair length was 100 per cent. Data for the 13 S.S.L. alatae were: Rhin./V 0-3 (mean of 25 antennae 0.24); M.T./7: 2 in three, 1 in three, 0 in seven; macula rather more variable than in the recoveries from the first test using series F + N, but generally rather large and solid. Progeny sampled on 19.vi.51; of 28 apterae, 25 had S.S.L. chaetotaxy and three S.S.S.; M.T. 7 distribution in the former was 2 in one, 1 in five, 0 in 19; in the latter it was 2 in one, 1 in none, 0 in two.

Gall series H. 6 recoveries. All had chaetotaxy S.S.L. Macula solid and extensive in all cases. M.T./7 absent in all. Rhin./V 0-4 (mean of ten antennae 1.40). Some progeny resulted, but the culture failed before any sample of adults could be collected.

Galls M.5, 7, 10. Offered *Aethusa* only. 6 recoveries. 5 of these were S.S.L., 1 L.L.L.; the latter and 2 of the former had the macula large and solid, the remaining 3 showed some reduction in size and intersegmental weakness. The long-haired alata had a single M.T./7; distribution in the short-haired alatae was: 1 in one, 0 in four. Rhin./V in long-haired specimen 1 and 2; in short-haired specimens 0-7 (mean of ten antennae 2.80). Colonization was barely successful; a single mature F.1 aptera was recovered on 2.vii.51, leaving a few small immature specimens. This aptera was S.S.L., without M.T./7. Test virtually negative.

(f) Recoveries from *Ranunculus*.

Gall series B. 2 recoveries. Hairs on ant. III medium to long, abd. 3 and 8 with long hairs. Macula extensive, solid, a solid black bar also present across abd. 2 in one specimen. M.T./7: 0. Rhin./V 1-10 (mean of four antennae 5.50). The resulting colony failed by 12.vi.51 through slug damage to the plant. Agreement with expectation 100 per cent.

Gall series D. 12 recoveries. Hairs on ant. III medium to longish, on abd. 3 longish to long, on abd. 8 long. Macula extensive, solid, and bars also present across abd. 1 and 2. M.T./7: 1 in two, 0 in 12. Rhin./V 5-10 (mean of 22 antennae 7.55). Progeny were all typical *ranunculi*. Agreement with expectation 100 per cent.

Gall series H. 2 recoveries, 1 was S.S.L. and 1 S.S.S. Colonization unsuccessful. Test negative.

Gall series I. 5 recoveries. Hairs on ant. III short to medium, on abd. 3 short to long, on abd. 8 long. M.T./7: 1 in two, 0 in three. Macula solid and extensive, bars also across abd. 1 and 2. Rhin./V 5-11 (mean of ten antennae 8.30). Progeny sampled 19.vi.51; all typical *ranunculi*. Agreement with expectation 100 per cent.

Gall K.1. At first offered *Angelica* only, without success; then *Ranunculus* only, on which settlement occurred. 5 recoveries. L.L.L. haired. M.T./7: 1 in one, 0 in four. Macula extensive, solid, bars also across abd. 1 and 2. Rhin./V 6-12 (mean of nine antennae 8.55). Progeny sampled 19.vi.51. All typical *ranunculi*.

(g) Recoveries from *Daucus*.

Gall series E. One recovery. S.S.L. M.T./7 absent. Rhin./V absent. Colonization failed. Test negative.

(h) Recoveries from *Smyrniium*.

Gall series E. 26 recoveries. 1 L.L.L., 2 S.S.S., 23 S.S.L. Of the latter, 11 have the macula very extensive and solid, 10 less extensive but solid or nearly so, 2 very markedly broken along the intersegments. This initial result suggests that *Smyrniium* is only weakly discriminated by species of the *crataegi* group, and is to

some extent acceptable to several forms. Progeny sampled 22.vi.51; all S.S.L. haired; M.T./7: 1 in two, 0 in 17. *Daucus carota* was later successfully colonized from this stock, the transferred stock producing alatae with a rather small, often broken macula, no rhinaria on ant. V and M.T./7 distribution: 1 in four, 0 in three. It seems likely that this stock was in fact *crataegi* Kltb. of Börner.

Gall series F (1st test) and N. 31 recoveries. 4 were L.L.L. (*lauberti*), with M.T./7: 1 in one, 0 in three; Rhin./V 0-1 (mean of eight antennae 0.25). Remainder were S.S.L., with macula solid and extensive in 22, appreciably broken in 5. The latter had M.T./7: 1 in three, 0 in two; Rhin./V 0. The former had M.T./7: 2 in four, 1 in seven, 0 in 11; Rhin./V 0-4 (mean of 44 antennae 0.36). Progeny of this transference, sampled on 18.vi.51, were all S.S.L., with M.T./7: 2 in one, 1 in four, 0 in nine.

Gall series F (2nd test). 11 recoveries. 2 were L.L.L. (*lauberti*), 1 with a single M.T./7, the other with none; Rhin./V 0-3 (mean of four antennae 1.25). 8 were S.S.L., with M.T./7: 1 in two, 0 in six; Rhin./V 0-2 (mean of 14 antennae 0.28). 1 was S.S.S. (of expected *inculta* type); this one was not in agreement with any gall from series F, and was of unknown origin. Progeny sampled on 19.vi.51 consisted of 12 L.L.L. (*lauberti*) type apterae and 9 S.S.L. apterae; M.T./7 distribution for the former being 1 in five, 0 in seven, for the latter 2 in two, 1 in four, 0 in three.

Gall series M. 4 recoveries. Two S.S.L., with M.T./7: 0, Rhin./V 0-2 (mean of four antennae 0.50), macula solid and extensive in 1, fairly so with a few slight weaknesses in the other. 2 S.S.[L.], with M.T./7 paired in 1, single in the other, Rhin./V 0-1 (mean of four antennae 0.25), macula much broken. These latter were of problematical origin. Progeny of this colonization were sampled on 5.vii.51 and 8.vii.51. All were S.S.L. Apterae had M.T./7: 1 in seven, 0 in 25. Alatae had M.T./7: 1 in two, 0 in 21; Rhin./V 0-3 (mean of 45 antennae 0.11); macula rather variable, generally rather extensive, but less so in some, and with occasional lines of intersegmental weakness.

(i) Recoveries from *Rumex*.

Rumex obtusifolius was offered in a number of tests (series A, B, C, D, H and I) as a control host, being the normal host of *Sappaphis radicola* (Mordv.), which does not belong to the group of aphid species under consideration. No recoveries of alatae were made; but in one instance a sparse colony of *Sappaphis* developed among a heavy infestation of *Myzus ascalonicus* Doncaster present on one plant of *Rumex*. This was in series A, and the culture persisted well into July. Apterae sampled proved to be long haired of typical *lauberti* facies.

(j) Recoveries from *Anthriscus sylvestris*.

This is the normal secondary host of *Sappaphis anthrisci* (Börner) which is associated with apple as primary host. It was also given as the host of a subspecies of *S. crataegi* by Börner (1950). A single S.S.L. alata was recovered from *Anthriscus* in gall series A, having no M.T./7 or Rhin./V. No colonization resulted, and the test was therefore negative. All other tests using *Anthriscus* (series B, C, D, F, H, I, K, L, M and N) were negative.

(k) Recoveries from *Choerophyllum temulum*.

This is the normal secondary host of *Sappaphis choerophylli* (Börner) which, like *anthrisci* Börner, belongs to the apple group of the subgenus *Dysaphis*. *Choerophyllum* was offered as a control host in series B, C, D, E, F and N. All these tests were negative for *Choerophyllum*, as was expected.

5 (iii). *Determinations of Original Gall Samples.*

Gall series A.

A.3, 4 and 8, together with one specimen from A.2, agreed with characters expected in *S. lauberti* (L.L.L., M.T./7 : 1 in one, 0 in five; Rhin./V 0-2 (mean of twelve antennae 0.33)). The remaining samples were all S.S.L., with macula extensive and solid, or with traces of intersegmental weakness.

Expectation was that hosts colonized should be (a) *Heracleum* and (b) *Daucus* and/or *Aethusa*.

(a) Was not realized; but long-haired progeny were ultimately recovered from *Rumex* (see 5 (ii)).

(b) Both *Daucus* and *Aethusa* were colonized, although the *Daucus* culture soon failed through death of the host.

This gall series had been selected for high colour rating of the galls (score 5). The contained nymphs were all pink.

Gall series B.

This series had been selected for low colour rating of the galls (scores 0-2). Contained nymphs were all of the pure grey colour previously noted in *ranunculi*. All alatae bore secondary rhinaria on ant. V, the lowest mean number per antenna in any sample being 4.63 (B.7), the highest 10.50 (B.5). The macula in all cases was large and solid, with only rather faint sculpturing visible which was not noticeably reticulate; and there was a constant more or less complete transverse bar across the second (and sometimes also the first) abdominal tergite.

Expectation that *Ranunculus* only would be colonized was realized.

Gall series C.

Colour rating of galls varied from 2 to 5. C.3, part of C.5 and C.10 agreed in characters with series B (*ranunculi*). C.2 and C.4 were of S.S.S. type; the former had M.T./7 : 0, Rhin. V 2-6 (mean 4.50); the latter had M.T./7 : 2 in two, 0 in one, Rhin. V 0-5 (mean 3.33). C.6 was L.L.L. haired, with M.T./7 : 0, Rhin. V 0-1 (mean 0.10). The rest were S.S.L., with macula variable in form and solidity, mean values for Rhin./V from 0 to 0.63 and most often without M.T./7.

Expectations for this series were:

(i) C.1, C.5b, C.7-9 : (a) *crataegi* Kltb.

(b) *kunzei* Börner.

or (c) *aethusae* Börner.

(ii) C.2, C.4 : *inculta* Wlk. (Börner).

(iii) C.6 : *lauberti* Börner.

(iv) C.3, C.5a, C.10 : *ranunculi* Kltb.

In the event there was a complete failure from this series of transferences. This could be in agreement with expectations (i) (a), (ii) and (iv), since *Petroselinum*, *Daucus* and *Ranunculus* were not among the choice offered; but no positive support was forthcoming for these expectations, and no support at all for expectations (i) (b), (i) (c) or (iii).

Gall series D.

These galls were selected for low colour rating (scores 0-2). The contained nymphs were pure grey, with in two cases a very slight lilac tinge. The resulting alatae resembled those of gall series B. Out of 25 alatae from all the galls of the series only one had a single marginal tubercle on abd. 7. Rhinarial numbers on ant. V varied from 3 to 11, with a mean of 6.98. Macula as in series B.

Expectation was that *Ranunculus* would be colonized. This was realized. No other host offered was accepted.

Gall series E.

A very mixed series. Gall colour ratings 2-5. It is convenient to consider the data for the various samples in tabulated form.

Gall	Colour score	Nymph colour	Characters of derived alatae						
			M.T./7			Rhin.V		Chaetotaxy	Macula
			2	1	0	Range	Mean		
E.1	3	Pinkish	0	0	5	0-3	0.50	L.L.L.	Extensive, solid.
E.2	4	Pinkish-grey	0	2	4	0-4	1.08	S.S.[L]. or [S].	Smaller, little weak anteriorly.
E.3	4-5	Lilac grey	1	1	1	0-5	1.67	S.S.L. or [L].	Some intersegmental weakness.
E.4	5	Pinkish	0	3	2	0-3	0.40	S.S.L.	Extensive, solid.
E.5	4-5	„	0	1	6	0-1	0.21	S.S.L.	„ „
E.6	5	„	0	0	3	0-1	0.17	S.S.[S].	Fairly extensive, solid.
E.7	2	Dove grey	1	2	2	0-4	0.50	S.S.L.	Some intersegmental weakness.
E.8	4	Pinkish*	0	0	3	0	0	S.S.L.	Very extensive, solid.
E.9	5	Lilac-grey to pinkish	0	1	4	0	0	S.S.L.	Extensive, solid.
E.10	5	Pinkish	0	1	4	0-2	0.40	S.S.L.	„ „ †

* One odd green nymph noted in gall. † Slight traces of intersegmental weakness in two specimens.

Expectations from these data were far from clear-cut. Colonization of *Heracleum* was expected from E.1, and this was realized in fact. No samples were recognized as *ranunculi*, and *Ranunculus* was not colonized. Colonization of *Petroselinum* was not expected from the morphology of the alatae examined; but as this colonization was apparently by a single alata, and a single odd green nymph had been noted in E.8, there seemed to be a possibility that these two circumstances were linked. The samples remaining were expected to be a mixture of some or all of the *crataegi-kunzei-aethusae* group. In fact *Aethusa* and *Smyrnum* were successfully colonized, *Pastinaca* less strongly so, and an initial infestation on *Daucus* failed through the death of the plant.

Gall series F.

This series was selected for high colour rating (all galls scored 5). F.1 and F.3 were long haired (L.L.L.); their respective M.T./7 distributions were; 1 in one, 0 in five (F.1), 2 in one, 1 in one, 0 in five (F.3); Rhin./V counts were: F.1 0-2 (mean of 12 antennae 0.58), F.3 0-4 (mean of 14 antennae 0.79). Remaining samples were all S.S.L., with macula more or less extensive and solid, mean Rhin./V varying from 0 to 0.57 and M.T./7 distributions ranging from 2/0, 1/0, 0/4 to 2/2, 1/3, 0/2.

Expectations were that *Heracleum* would be colonized by the long-haired forms, and that the remaining samples would prove to belong to one (or possibly two) of the *crataegi-kunzei-aethusae* complex. In fact, *Heracleum*, *Aethusa* and *Smyrnum* were colonized in both tests performed with this gall series, while *Petroselinum*, *Pastinaca*, *Daucus*, *Angelica*, *Ranunculus* and *Choerophyllum* were not infested.

Gall series G.

Only four galls were used from this series. G.1, an S.S.S. sample with green nymphs, was expected to be *inculta*, was offered *Petroselinum* only and successfully colonized it. G.5 and G.10 were S.S.L.; their respective M.T./7 distributions were: 1 in one, 0 in one (G.5), 0 in three (G.10); Rhin./V counts were: G.5 0-3 (mean of four antennae 1.00), G.10 0-2 (mean of six antennae 0.67). The macula in these two samples was moderately extensive, sometimes weakened anteriorly or intersegmentally. G.8 was L.L.L., with M.T./7 distribution 2/0, 1/2, 0/2, no secondary rhinaria on V and with a solid and extensive macula. These latter three samples were together offered *Heracleum* only. A sparse colonization resulted, the progeny agreeing most closely with the characters of G.8.

Gall Series H.

H.3, 4 and 8 failed to produce any alatae. H.1 and 2 from gall and nymph colour and morphology of the alatae were expected to be *ranunculi*. H.5-7 were S.S.L.; all had the mean Rhin./V value 0.50 (four antennae in each case), with ranges 0-2, 0-1 and 0-2 respectively; the macula in each sample was extensive and solid; and M.T./7 were absent except for a single unpaired one in H.7.

Alatae from these galls were offered nine hosts (see 5 (i)); initial colonization of *Ranunculus*, *Aethusa* and *Pastinaca* occurred, and progeny resulted on *Aethusa*, but all cultures failed very quickly. No satisfactory conclusions could be drawn, although the production of young on *Aethusa* was in agreement with the morphology of H.5-7, and the colonization of *Ranunculus* agreed with expectation for H.1 and 2.

H.9 and 10 were offered *Pastinaca* only. This was rejected, and subsequent examination showed that the alatae were morphologically identical with *S. angelicae* having L.L.L. chaetotaxy, M.T./7 distribution 2/0, 1/10, /5, Rhin./V 2-7 (mean of twelve antennae from both galls 5.08). Colour rating of both these galls was 5.

Gall series I.

Gall colour ratings variable (1-5). I.1 and 2, with low gall colour ratings, L.L.L. haired, Rhin./V 6-11 (means of four antennae 6.75 and 9.25), M.T./7: 0, macula extensive and solid, and with a solid bar across abd. 2, were expected to be *ranunculi*. I.9, with gall colour 3, was a similar sample, but with M.T./7 distribution 2/0, 1/2, 0/1 and Rhin./V 4-7 (mean of six antennae 4.83). I.5 and 6, with gall colour rating 3-4, produced alatae with rather similar characters, but with no bar across abd. 2 and a more marked reticulation of the cuticle of the dorsal macula. The other data for these alatae were: chaetotaxy L.L.L., M.T./7: 2/0, 1/0, 0/2 and 2/0, 1/1, 0/3 respectively, Rhin./V 10-15 (mean of four antennae 12.5) and 5-9 (mean of eight antennae 6.5) respectively. These samples were expected to be *angelicae*. I.8 and 10 were typically *lauberti* in character: gall colour 4-5, chaetotaxy L.L.L., macula solid and extensive, M.T./7: 2/0, 1/3, 0/0 and 2/0, 1/0, 0/4 respectively and Rhin./V 0-3 (mean of six antennae 0.83) and 0-2 (mean of eight antennae 0.63) respectively. Single alatae from I.4 and 7 were S.S.L. haired (that from I.4 being apparently an odd one from a typical *ranunculi* gall with grey nymphs!), and these alatae were ascribed tentatively to the *crataegi-kunzei-aethusae* complex.

The choice offered to series I alatae did not include *Daucus* or *Aethusa*. *Ranunculus*, *Angelica*, *Heracleum* and *Pastinaca* were colonized, the last-named by long-haired aphids agreeing with *lauberti* in characters.

Gall series K.

Only four galls used. The characters of K.1-3 predicted their identities as *ranunculi*, *kunzei* and *lauberti* respectively ; appropriate hosts only were offered, and in each case the expected colonization resulted. In the case of K.1 *Angelica* had been previously offered and rejected. Alatae of K.3 had an abnormally high Rhin./V value for *lauberti* (0-6, mean of eight antennae 3.25), but otherwise agreed well with the characters predicted from the field collections.

K.4 alatae were rather shorter-haired than is usual in *lauberti*, but none the less colonized *Heracleum* rather reluctantly from a choice of *Heracleum*, *Pastinaca*, *Daucus* and *Anthriscus*. These alatae were without rhinaria on V or marginal tubercles on abd. 7 in four specimens kept as controls.

Gall series M.

M.1 and 2 yielded no alatae, so that their expected identity (*ranunculi*) was not confirmed. The characters of the remaining gall samples are summarized below :

Gall	Colour score	Nymph colour	Characters of derived alatae						
			M.T./7			Rhin./V		Chaeto-taxy	Macula
			2	1	0	Range	Mean		
M.3	4	Pinkish	0	2	3	0-6	2.00	S.S.L.	Extensive, solid.
M.4	5	Pink	0	1	4	0-4	0.60	L.L.L.	" "
M.5	5	Green	0	0	2	0-6	2.50	[L.L.]L.	Fairly extensive, solid.
M.6	5	Pink	0	0	5	0-1	0.20	S.S.L.	Extensive, solid.
M.7	5	Green	0	0	2	0-2	0.75	L.L.L.	" "
M.9	5	Pink	0	0	4	0	0	[L.L.]L.	" "
M.10	5	Green	0	0	2	0-2	1.50	S.S.L.	Extensive, nearly solid.

Gall M.8 also produced no alatae, but no prediction was possible from gall and nymph colour. Galls M.4, 5 and 9 were more or less intermediate in hair length, but tending towards long-hairedness in the alatae produced.

The probable identities of series M alatae were hard to assess, owing to considerable "mixing up" or recombination of the characters arrived at from study of field material. In fact the only hosts colonized by the pink nymph alatae from galls M.3, 4, 6 and 9 were *Pastinaca* and *Smyrniun* ; but some of the alatae recovered from these two hosts did not agree with any of the gall samples recorded above (suggesting either contamination of the culture or mixed gall populations in some of the series M galls). *Heracleum*, although offered, was not colonized, and no L.L.L. recoveries were made. The green nymph alatae from M.5, 7 and 10 were offered only *Aethusa*, and only produced one recoverable apterous progeny, which was S.S.L. (M. 10?). The result should probably be treated as a negative one.

Gall series N.

Only two galls collected, both with colour rating 5. Both produced L.L.L. alatae, with M.T./7 distributions 0 and 2/1, 1/2, 0/3 respectively, and Rhin./V

ranges 0-2 (mean of six antennae 0.83) and 0-3 (mean of 12 antennae 0.50) respectively. Both samples were apparently *lauberti*. The alatae were incorporated into the first test of gall series F, in which *Heracleum* was in fact colonized. It is not possible to ascribe this colonization with certainty to series N galls, since *lauberti* also occurred in series F; but the result is not in conflict with expectation.

6. PRELIMINARY CONCLUSIONS FROM 1951 EXPERIMENTS.

The preliminary conclusions drawn from the foregoing series of tests may once more be conveniently considered under the headings of the aphid species concerned.

Sappaphis lauberti (Börner).—Alatae exhibiting the characters of *lauberti* as assessed from field collections on *Heracleum* were produced from a small but significant percentage of the galls collected. Colour rating of these galls was mainly 5, but some with ratings of 3 and 4 were also recorded. Nymph colour in all the positively established samples of *lauberti* was uniformly pinkish or pink-tinged, and there was distinct wax pulverulence in all cases. One or two samples referred to *lauberti* were slightly atypical in some character (e.g. gall K.3, abnormally high rhinarial counts on ant. V; gall K.4, abnormally short antennal and abdominal hairs). Host choice in general agreed very well indeed with expectation. Anomalous colonizations by aphids with *lauberti* characteristics were recorded on *Pastinaca* (gall series I) and *Rumex* (gall series A); the former host has on occasions been found infested by *lauberti* in the field.

S. angelicae (Koch).—Alatae agreeing in morphology with previously collected material of *angelicae* were produced only from galls H.9 and 10 and I.5 and 6. The two former samples were offered only *Pastinaca*, which was rejected, and their identity was therefore not definitely confirmed. Colonization of *Angelica* by aphids identical with the I.5 and 6 gall samples did take place, however; and both the recoveries after transference and the midsummer alate progeny agreed with the two gall samples in the frequency distribution of rhinarial numbers on ant. V, while apterous progeny agreed with wild collected apterae of *angelicae*.

The galls from which *angelicae* was obtained had colour rating 3-5, and the contained nymphs in all cases were pinkish, with distinct wax pulverulence. In contrast to the alatae of *S. ranunculi* (see below) those of *angelicae* showed for the most part a marked reticulate sculpture of the dorsal macula, while the second abdominal tergite was adorned with at most a pair of small spinal sclerites, and never with a transverse bar across the spinal region.

S. ranunculi (Kltb.).—Previous observations were confirmed. Colonizations were obtained on *Ranunculus* only from gall series containing galls of colour rating 0-3 inhabited by pure grey nymphs. These nymphs produced alatae with rather numerous rhinaria on ant. V. Conversely, in gall series consisting only of pale galls containing grey nymphs only *Ranunculus* was colonized.

Examination of *ranunculi* alatae further indicated that they could be separated from those of *angelicae* (see above) by the presence of a more or less complete transverse sclerotic bar across the second (and sometimes also the first) abdominal tergite, and by the much less conspicuous (often quite absent) and less reticulate-looking sculpture of the dorsal macula.

S. aethusae (Börner).—In spite of the failure under closer scrutiny of the morphological discriminants given by Börner the evidence for a discrete biological race or subspecies of the *crataegi* complex on *Aethusa* was strengthened by the results of the 1951 experiments. Alatae from gall series A, E, F and H which colonized *Aethusa* all agreed in having an extensive, solid dorsal macula, short hairs on the antennae and 2nd/3rd abdominal tergites and rather long acute hairs on the 8th abdominal tergite. Gall and nymph colour ratings agreed closely with those of *lauberti*. Recolonization tests at midsummer using alatae derived from gall series E and bred on *Smyrniurn* suggested that this is a host which may be accepted by *aethusae*. A

similar test using alatae derived from a field collection on *Torilis japonica* suggested that this plant could be an alternative secondary host of *aethusae* in nature.

S. kunzei (Börner).—Only one gall sample apparently referable to *kunzei* was collected (K.2). The identity was predicted from the rather markedly broken macula of the alatae, and was supported by the result of a single non-choice test in which only parsnip was offered. In view of the absence of choice this result is treated with reserve. The gall had a colour rating of 4, and nymph colour was recorded as lilac-grey with fairly definite wax powdering. Results from gall series M were inconclusive.

S. crataegi (Kltb.).—Almost only negative evidence was obtained, in the complete failure of any tests including *Daucus* among the hosts offered. An exception was gall series A, where an expected initial colonization of *Daucus* did result, but failed through the death of the plant.

S. inculta (Wlk.) Börner.—Galls producing alatae with a greater or less expression of the characters expected for *inculta* were recorded in series C, E and G. The number was however too small for completely satisfactory conclusions to be drawn. The galls in question had colour ratings 3-4, with nymph colour varying from green through greenish to pinkish-olive, with rather little wax powdering. The differences between alatae of these samples and those of *crataegi sensu latiori* (including *aethusae* and *kunzei*) were less clear cut than in material from secondary hosts in the field. *Petroselinum* was colonized successfully in two instances, while consistent rejection of this host in two sets of tests with gall series F and N indicated that it is not acceptable at least to *lauberti* or *aethusae*.

7. THE 1952-54 EXPERIMENTAL PROGRAMMES.

The preliminary conclusions from the 1951 series of experiments removed the necessity for further specific research on *Sappaphis lauberti* (Börner), *S. angelicae* (Koch) and *S. ranunculi* (Kltb.), all of which had given conclusive proof (having regard to the technical limitations of the method used) of their objective reality as members of the hawthorn *Sappaphis* community.

Questions remaining unanswered, or in an unsatisfactory state, after the 1951 experiments had been analysed related mainly to the status of the other four species recognized by Börner: *Sappaphis aethusae*, *S. kunzei*, *S. crataegi* and *S. inculta*. The first named was in fact the commonest member of the whole group in the area where galls were collected in 1951, and a fairly definite picture of its morphological and gall characters was obtained; but it remained necessary to relate it more definitely to *kunzei* and *crataegi*, apterae of which appeared to be inseparable from those of *aethusae* by any reliable character. The other three forms had not been found in sufficient numbers among the 1951 gall samples to justify any definite conclusions.

The programmes carried out in 1952-54 were therefore aimed primarily at obtaining data on these four species or forms, and pale *ranunculi*-type galls were ignored in the collection of spring migrant material. Particular importance was attached to the examination of nymph colour in the galls collected, in view of Börner's use of this character as a discriminant between *kunzei* and *crataegi*.

Divergences from the 1951 methods in the three following years were as follows:

1952. The "pooled gall" method was again used, but pooling was modified to group together alatae derived from nymphs of similar colour as well as those from a given gall series.

1953. The "pooled gall" system was replaced by a series of tests of alatae from individual galls, thus avoiding the modifying effect on behaviour of the presence of other alatae of different species.

1954. A mixture of "pooled gall" and individual tests was performed, the pooling being determined on the preliminary data recorded from the gall contents and the low-power examination of the early emergences of alatae.

8. SUMMARY OF RESULTS (1952).

Data for the 1952 series of experiments are presented in the same form as those for the 1951 series.

An additional host plant abbreviation not employed in the 1951 experiments is:
Ap *Apium graveolens*, f. *dulce* Mill.

8(i). Gall Data.

TABLE II.—Gall sample data and choice tests (1952).

Gall series	Locality	O.S. grid ref.	Gall colour	Nymph colour	Wax	Host choice							
						Ae	Da	Pa	Pe	Ap	He	Ang	
P.1-2, 5-10	Cambridge	452573	3-5	Pink	2	—	+	(+)	—	—	
P.3-4	„	452573	3	Green	2	—	—	(+)	+	+	
Q.1, 3-6, 8-10	„	444586	3-5	Pure grey to pink	2-3	—	+	..	—*	—†	—	—	
Q.2, 7	„	444586	3-4	Green	2	—	—	(±)	+	+	
R.1-3	„	454570	4	Pinkish-grey	(?)	+	—	—	..	—	
T.1-10	„	443586	3-4	Greenish-grey to pinkish	2-3	(+)	—	—	+	—	—	..	
U.1-3	Little Wilbraham	547587	4	Pink	2	—	—	—	..	—	

* Not Q.1. † Q.1 only.

- Notes on Table II:
- 1. P.3-4 and Q.2 and 7 were combined in one test.
 - 2. R.1-3 and U.1-3 were combined in one test.
 - 3. Positive results refer only to cases where F.1 progeny were recovered or surviving at 26.v.52.
 - 4. Intrusive populations of *Myzus ascalonicus* Donc. were present on some test plants. They were particularly heavy on *Aethusa* colonized in the R + U and T series tests.
 - 5. Additional abbreviation:
Ap *Apium graveolens* f. *dulce* Mill.

8 (ii). Data from *Alatae* and F.1 Recovered from Secondary Hosts after Colonization.

(a) Recoveries from *Daucus*.

Gall series P (pinkish nymphs). 24 *alatae* recovered. All were S.S.L. haired, with a fairly extensive, solid dorsal macula. 7 out of the 24 had an unpaired marginal tubercle on the seventh abdominal tergite. Secondary rhinaria on ant. V ranged from 0-3, mean 0.23. These *alatae* agreed with the observed characters of *crataegi* Kltb. from field collections. 12 F.1 apterae exhibited similar chaetotaxy to the *alatae*. M.T./7 distribution was 2/0, 1/1, 0/11. The antennal flagellum varied in length from about one-third to a little less than half the body length. These apterae agreed well with *crataegi* from field collections.

Gall series Q (pinkish nymphs). 2 recoveries. Hair characters and macula as for series P recoveries. M.T./7 absent. Rhin./V 0. 10 F.1 and F.2 apterae

agreed with those from series P except that the antennal flagellum varied from about two-fifths to just over half the body length. Agreement with *crataegi* was again good.

(b) Recoveries from *Pastinaca*.

Gall series P+Q (green nymphs). 1 recovery. Chaetotaxy S.S.S. M.T./7 absent. Rhin./V 9 and 9. 2 F.1 apterae were S.S.S. and S.S.[L?] respectively. Both had a single unpaired marginal tubercle on abd. 7. Antennal flagellum length varied from two-fifths to a little less than half body length. This small group of three specimens agreed on the whole with the observed characters of *S. inculta* Börner rather than with those of *kunzei*. Colonization of *Pastinaca* could not be considered as definitely positive.

Gall series P (pink nymphs). 12 recoveries. Two had shortish hairs on the eighth abdominal tergite; the remainder were S.S.L. haired. M.T./7 distribution was 2/2, 1/3, 0/7. Dorsal macula fairly to quite solid. Rhin./V 0-2, mean 0.17. 6 F.1 and F.2 apterae were S.S.L. haired, without marginal tubercles on abd. 7 and with the antennal flagellum from three-eighths to a little over half body length. These specimens agree rather more closely with the expectation of characters for *crataegi* than with those for *kunzei*, though the apterae could belong to either form. The colonization was a weak one, and the question of whether it should be reckoned as agreeing with or contrary to expectation remained open.

(c) Recoveries from *Aethusa*.

Gall series R+U. 12 recoveries. 11 of these were long haired, with a rather extensive macula, solid in 6 and somewhat broken in 5. One out of these had an unpaired marginal tubercle on abd. 7. Rhin./V 0-2, mean 0.10. The twelfth alata was S.S.L. haired, with extensive, solid macula, an unpaired marginal tubercle on abd. 7 and no secondary rhinaria on ant. V. 10 F.1 and F.2 progeny agreed in chaetotaxy with this last alata; M.T./7 absent; antennal flagellum four-elevenths to six-elevenths of body length. The apterae and twelfth alata agreed well with the known characters of *S. aethusae* (Börner). The other 11 alatae, which agreed with the characters of gall samples U.1-3, produced no progeny which survived, and agreed most closely with the characters of *S. lauberti* (Börner). It should be noted that *Heracleum* was not offered in this choice test.

Gall series T. 3 recoveries. 2 of these were S.S.S. haired, with a somewhat broken macula, M.T./7 distribution 2/1, 1/0, 0/1, and Rhin./V 6-8, mean 7.30. The third specimen was S.S.L. haired, with a solid and extensive macula, M.T./7 absent and Rhin./V also absent. 10 F.1 and F.2 apterae were rather evenly divided into groups corresponding with the two types of alatae. 6 were S.S.S. and 4 S.S.L. haired. The M.T./7 distributions of the two groups were 2/1, 1/3, 0/2 and 2/0, 1/1, 0/3 respectively. The short-haired group here represented an anomalous colonization, their characters agreeing with those of *S. inculta* (Wlk.) Börner. The aphids with long hairs on the eighth tergite agreed well with *S. aethusae* (Börner).

(d) Recoveries from *Petroselinum*.

Gall series P+Q (green nymphs). No alatae recovered. 7 F.1 and F.2 apterae recovered from colonies resulting from this transference were all S.S.S. haired, with M.T./7 distribution 2/4, 1/3, 0/0. The antennal flagellum ranged in length from a little less than two-fifths to not quite half the body length. These apterae were typical of *inculta*, and agreed well with expectation.

Gall series T. 2 recoveries. One clearly S.S.S. haired, the other with somewhat longer hairs on the eighth tergite. Both with an unpaired marginal tubercle on seventh tergite. Rhin./V 4-8, mean 5.50. Dorsal macula rather extensive and solid. 10 F.1 and F.2 apterae were all S.S.S. haired; M.T./7 distribution 2/2, 1/7, 0/1.

The 2 alatae agree fairly well with *inculta*, though the longer hairs on the eighth tergite in one, and the density of the macula, are not typical. The apterae agree well with expectation for *inculta*.

(e) Recoveries from *Apium*.

Gall series T. 1 recovery. Chaetotaxy S.S.L. Macula fairly extensive, rather solid. M.T./7 absent. Rhin./V 1 and 8. No progeny reached maturity. This recovery suggested *inculta* only in its large rhinarial number on ant. V. Its other characters were closer to those of *crataegi* s.l. Since *Daucus* and *Pastinaca* were rejected altogether in this test series it seemed possible that this was an atypical specimen of *aethusae*.

Gall series P+Q (green nymphs). No recoveries of alatae. 6 F.1 and F.2 apterae were S.S.S. haired. M.T./7 distribution was 2/5, 1/1, 0/0. The antennal flagellum length varied from a little over one-third to a little less than half body length. These apterae agreed well in chaetotaxy and M.T./7 distribution with observed data for *inculta*.

(f) Recoveries from *Heracleum*.

Gall series T. 1 recovery. Chaetotaxy S.S.[L?], an unpaired marginal tubercle on abd. 7, Rhin./V 1 and 5, dorsal macula somewhat broken. These characters agreed rather well with those of *inculta* apart from the hair length on the eighth tergite. No progeny resulted, and the result was accordingly classed as negative.

8 (iii). Determinations of Original Gall Samples.

Gall series P.

This series was divided into galls containing pinkish nymphs and those containing green ones. The latter were combined with similar galls from series Q for choice test purposes. Morphologically the green nymph alatae from P.3 and 4 agreed markedly with the expected characters of *inculta*, i.e. a somewhat anteriorly broken macula, paired or unpaired marginal tubercles on abd. 7 in all the alatae sampled as controls, and 1-9 (mean 5.33) secondary rhinaria on ant. V. Expectation was therefore that *Petroselinum* and/or *Apium* should be colonized in the choice test using this group of galls, and this in fact happened.

The pink nymph gall samples collected from the same stretch of garden hedge were morphologically less homogeneous. All were short-haired on antennae and abdominal dorsum, but the hairs on the eighth tergite were rather variable in length, from long to short. Rhin./V values ranged from 0 to 4, the individual sample means being respectively 1.67, 0, 0.17, 0.50, 0.83, 2.00, 2.00 and 0.67 per antenna. Except for a single unpaired tubercle in one specimen from P.5, M.T./7 were absent. The macula was rather extensive, varying from nearly solid to broken at some intersegments. This mixture of characters gave no very clear basis on which to forecast the choice of host; the successful colonization of *Daucus* and the less successful settlement on *Pastinaca* showed that at least part of the population was *crataegi* Kltb., with a possible admixture of *S. kunzei* Börner.

Gall series Q.

A similar division into galls containing green and non-green (some of the latter were not distinctly pinkish) nymphs was made in this gall series. Green nymph alatae from Q.2 and 7 had short to moderate length hairs on the eighth tergite. Only one alata from each gall was taken as a control sample; that of Q.2 had a single unpaired M.T./7, and 0 and 2 secondary rhinaria on V, while that of Q.7 was without M.T./7, and had Rhin./V 5 and 9.

The non-green nymph samples were very variable in colour, from pure grey through greenish-grey with pinkish thorax to pinkish-grey or pinkish. Of these, Q.1, with pure grey nymph colour, apparently belonged morphologically to *inculta*, and the colour difference was probably due to its having somewhat heavier wax powdering than either Q.2 or Q.7. These alatae from Q.1 were S.S.S. haired, with M.T./7 distribution 2/0, 1/2, 0/1 and rhinaria on ant. V 3-11 (mean 7.20). The macula was quite solid, however. This sample was offered a choice containing *Apium* but not *Petro-selinum*. No colonization resulted.

The remainder of the series produced alatae with S.S.L. chaetotaxy, apart from three odd specimens in which the hairs on the eighth tergite were verging on the shorter length of *inculta*. Except in Q.5 the macula was extensive and quite solid. Rhinarial numbers on ant. V varied from 0 to 7, with individual sample means as follows : Q.3, 0.33; Q.4, 0.25; Q.6, 1.33; Q.8, 0; Q.9, 0.50; Q.10, 6.00. In Q.5 the fifth antennal joints were missing in the sole control specimen. Q.6 had M.T./7 distribution 2/0, 1/2, 0/1; tubercles were absent from all the other samples.

The characters of Q.3, 6, 8 and 9 suggested a probability that they were either *crataegi* Kltb. or *aethusae* Börner. It seemed possible that Q.5 might be *kunzei* Börner, while Q.10 was anomalous, the sole control specimen having a very high rhinarial number on ant. V. In the event only *Daucus* was colonized successfully by this series, which agreed with the assumption made for Q.3, 6, 8 and 9. The characters of the recoveries agreed with those of these four gall samples. No recoveries agreeing with Q.5 or Q.10 were made.

Gall series R.

All the alatae of R.1-3 were S.S.L. haired. The macula was extensive and solid in R.1 and 2, broken at some intersegments in R.3. The latter sample had M.T./7 distribution 2/1, 1/2, 0/0, while tubercles were absent from R.1 and 2. Rhin./V values varied from 0 to 3, sample means being 1.00, 0.25 and 0 respectively. The characters of R.1 and 2 suggested identity with *crataegi* or *aethusae*. R.3 apart from the marginal tubercle incidence might be *kunzei*.

The results of the choice test made with alatae from series R and series U together were positive to *Aethusa* only. *Apium*, *Daucus* and *Pastinaca* were rejected. Only one recovery agreeing with series R was made, and this agreed in the shape of the macula with R.1 and 2.

Gall series T.

The alatae of this series showed a strong mixture of characters. Chaetotaxy varied from S.S.S. to S.S.L., and nymph colour from greenish-grey through pinkish-grey to pinkish. Rhin./V numbers varied from 0-13, with sample means as follows : T.1, 5.20; T.2, 5.63; T.3, 0.75; T.4, 2.50; T.5, 5.92; T.6, 1.63; T.7, 0.50 (1 specimen), T.8, 6.50; T.9, 7.50; T.10, 6.25. The value given for T.6 is an overall mean value; the sample was derived from two fundatrices in one gall, and these two subsamples had probable separate means of 2.40 and 0.33 respectively. Macula generally solid, except for T.1, 4, 10 and one specimen from T.2, in which some intersegmental weaknesses were present. M.T./7 generally absent, except in T.5 and T.10, which had distributions 2/1, 1/4, 0/1 and 2/0, 1/2, 0/0 respectively; and in single specimens of T.2 and 8, in which unpaired tubercles occurred.

The characters of this gall series posed a considerable problem. In a number of the galls alatae exhibiting one or more of the expected characters of *inculta* were produced. Correlation between these characters was weak, however, and in the majority of cases the balance of evidence lay toward the *crataegi* group proper (e.g. *crataegi* and *aethusae*).

The actual results of the choice tests with series T were a positive colonization of *Petroselinum* and a weak colonization of *Aethusa*, the latter in the presence of heavy contamination by *Myzus ascalonicus* Doncaster. *Daucus*, *Pastinaca*, *Heracleum* and *Apium* were rejected. The recoveries from *Petroselinum* agreed rather well with *inculta*, i.e. they were apparently drawn from those galls exhibiting the greatest correlation of *inculta* characters, such as T.5. Of three recoveries from *Aethusa* two showed more or less strongly the characters of *inculta* and one those of the *crataegi* complex, probably from T.3, 6 or 7. The progeny which resulted on both hosts agreed with their alate parents. It was noticeable that recoveries agreeing in characters with the anomalous samples T.2, 8 and 9 were almost non-existent. One such alata was recovered from *Apium*, but no colonization resulted. A single recovery of more definite *inculta* type was made from *Heracleum*, but here again no progeny resulted.

Gall series U.

U.2 produced no alatae. The only two galls in this series which produced alatae, U.1 and 3, were combined with series R for choice test purposes. Both were L.L.L. haired, with a fairly to quite solid macula, M.T./7 absent, Rhin.V 0-2, with sample means 0.40 and 0.75 respectively. The characters of this material were clearly those of *lauberti*. *Heracleum* was not offered in the choice test. 11 recoveries of alatae agreeing with series U were made from *Aethusa*, but no colonies resulted. *Pastinaca*, *Daucus* and *Apium* were rejected. This result was in accordance with expectation.

8 (iv). Points for Later Consideration.

The following points arising from the experiments of 1951-52 are noted here, but discussion of them will be postponed until the general discussion of the whole programme and its results (p. 677).

(1) It is noticeable that the characters regarded as typical of *inculta* do not show a very high and consistent degree of correlation; in other words, samples not infrequently occur in which one or more of the typical characters of *inculta* may be missing while the others are clearly recognizable; or in which a single character may be strongly suggestive of *inculta*, while the morphology as a whole does not support this identity. This is well illustrated in various members of gall series P, Q and T, particularly the last-named.

(2) Following on from (1), anomalous samples such as Q.10, T.2, T.8 and T.9, which exhibit dissociated *inculta* characters, tend not to be represented among recoveries from host plants after choice tests.

(3) Taking 1951 and 1952 together, it is noticeable that not infrequently series of galls collected from a single bush or close together on a small stretch of hedge, and in which very definite samples of *inculta* (i.e. with high correlation of the typical *inculta* characters) were present, contained also one or more samples which possessed *inculta* characters in a more or less dissociated degree; e.g. gall series G, Q and T. Such samples did not appear among homogeneous gall populations from which "true" *inculta* was absent, with the possible exception of series E (1951), where *inculta* galls may well have been present in the natural population, although not included in the sample, since many more galls were present than were in fact collected.

(4) In Q.1 and gall series T *Apium* was not successfully colonized by aphids with *inculta* characters, although in series T *Petroselinum* was colonized. In P+Q (green nymph) samples *Apium*, though colonized, was only reluctantly so, and the colonies were less successful than those on *Petroselinum*.

9. SUMMARY OF RESULTS (1953).

9 (i). *Gall Sample Data.*

Only fourteen galls were employed in this series of experiments. They were designated individually by a double letter combination, AA to AN inclusive. Galls AA to AM were collected at O.S. grid ref. 452573 (the same locality as series E (1951) and P (1952)), and AN at O.S. grid ref. 454571 (the same as series F (1951)). The galls were tested singly instead of in batches, the method used being otherwise the same as in 1951-52.

TABLE III.—Gall data and choice test results.

Gall	Gall colour	Nymph colour	Wax	Host choice range							
				Ae	To	Pa	Da	Pe	Ch	Sm	He
AA	2	Greyish-pink	2	(+)	(±)	—	+	—
AB	4-5	Strong pink	2	+	+	—	—
AC	4-5	„ „	2	+	+	—	—
AD	4-5	Pinkish-grey	3	—	—
AE	2-3	Greyish-pink	2	—
AF	3	Pinkish-grey	1	+	+	..	—	—
AG	3-4	„ „	2	—	—	—	—
AH	5	Greyish-pink	3	+	+
AI	4	Pinkish-grey	3	+	+	—
AJ	5	Greyish-pink	2	—
AK	4	Pink	2	+	(+)	—	—	—	—	—	—
AL	3-4	Strong pink	1	+	+	—
AM	3-4	„ „	1	—	—	—
AN	4-5	Pinkish-grey	2	—

Additional host plant abbreviation :
To *Torilis japonica* (Houtt.) DC.

9 (ii). *Data from Recoveries.*

As the galls have been tested singly it is not necessary to in a separate section of discuss the morphology the alatae recovered.

9 (iii). *Determinations of Original Gall Samples.*

Gall AA.

Chaetotaxy S.S.L. Macula extensive, but with traces of weakness along inter-segments, particularly intersegment 3/4. M.T./7 absent. Rhin./V 0-4, mean of 17 antennae 0.53. This sample colonized *Daucus* strongly, indicating the identity of the sample as *crataegi* Klth. *Aethusa* and *Torilis* were also weakly colonized ; the culture on *Aethusa* became stronger by mid-June, but that on *Torilis* remained

precarious. *Aethusa* specimens were of normal size, those of the *Torilis* colony were noticeably smaller. The size ranges of the F.1 apterae on the three hosts were :

<i>Daucus</i>	.	.	Body length	1.82-2.24 mm.
<i>Aethusa</i>	.	.	" "	1.78-2.10 mm.
<i>Torilis</i>	.	.	" "	1.54-1.78 mm.

F.1 progeny on *Daucus* became mature appreciably sooner than those on *Aethusa*, being in their fourth instar by 4 June, while the aphids on *Aethusa* were still in the second instar.

Gall AB.

Chaetotaxy S.S.L. Macula extensive, solid, except for very slight intersegmental breaks in three specimens. Unpaired marginal tubercles on abd. 7 in four out of 19 specimens, remainder with none. Rhin./V 0-3, mean of 37 antennae 0.35. *Aethusa* and *Torilis* only were colonized, *Pastinaca* and *Daucus* being rejected. A few young were deposited on *Daucus*, but none reached maturity. Progeny on *Torilis* lagged behind those on *Aethusa* in development, and F.2 larvae were whitish, lacking a pinkish tinge present in F.2 larvae on *Aethusa*. The sample was evidently *aethusae*.

Gall AC.

Chaetotaxy S.S.L. Macula extensive, solid. M.T./7 unpaired in one, absent in two out of three. Rhin./V 0-2, mean of six antennae 0.83. The colonization reaction of this sample repeated that of AB, both *Daucus* and *Pastinaca* being completely rejected. The *Torilis* colonists after a slow start caught up with the *Aethusa* colonies by 16 June 1953, when F.1 apterae were distinctly more waxy on the dorsum than the F.1 on *Aethusa*. The sample was evidently *aethusae*.

Gall AD.

Chaetotaxy S.S.L., macula extensive and solid. M.T./7 absent in the two available alatae. Rhin./V 0. Offered *Daucus* and *Pastinaca* only. Both were rejected. The inference is that this sample was also *aethusae*, but the evidence is purely negative.

Gall AE.

Chaetotaxy S.S.S., macula only moderately solid. M.T./7 distribution 2/1. 1/1.0/0. Rhin./V 1-10, mean of four antennae 6.25. Only offered *Daucus*, which was rejected. This result was in accordance with the morphology of the alatae, which were apparently typical *inculta*.

Gall AF.

Chaetotaxy S.S.L., macula extensive and solid. M.T./7 absent. Rhin./V 0-2, mean of ten antennae 0.70. Colonization was a repetition of that in AB and AC, *Aethusa* and *Torilis* being successfully colonized and *Daucus* and *Petroselinum* rejected, although six or seven first instar larvae, the progeny of two alatae, were found on *Petroselinum*; these failed to reach maturity. F.1 apterae on *Aethusa* were slightly larger than those on *Torilis*. Sample referable to *aethusae*.

Gall AG.

Chaetotaxy S.S.L., macula extensive and solid. M.T./7 absent. Rhin./V 0-2, mean of five antennae 0.80. This sample failed to colonize *Heracleum*, *Pastinaca*, *Daucus* and *Petroselinum*; such a result indicates that the sample was *aethusae*, but as *Aethusa* was not offered the biological evidence is negative.

Gall AH.

Chaetotaxy S.S.L., macula rather extensive and solid. M.T./7 distribution 2/1, 1/1, 0/6. Rhin./V 0-1, mean of six antennae 0.33. The choice offered was between *Aethusa* and *Torilis* only. Both were successfully colonized, the colony on *Aethusa* being rather stronger than that on *Torilis*, and the F.I developing faster on the former host. The sample was apparently referable to *aethusae*, the conclusiveness of the result being slightly reduced by the absence of other hosts in the choice test.

Gall AI.

Chaetotaxy S.S.L., macula extensive and solid. M.T./7 absent. Rhin./V 0. This sample colonized *Aethusa* and *Torilis*, the former more strongly than the latter. *Petroselinum* was refused. The sample was evidently *aethusae*.

Gall AJ.

Chaetotaxy S.S.L., macula extensive and solid (one alata only). M.T./7 absent. Rhin./V 0. Offered *Pastinaca* only; result negative. Perhaps *aethusae*, but evidence inconclusive.

Gall AK.

Only one alata in reference sample, with characters as for AJ. The choice offered was *Aethusa*, *Torilis* (both accepted), *Daucus*, *Pastinaca*, *Heracleum*, *Petroselinum*, *Choerophyllum* and *Smyrnum* (all rejected). This established the identity of the sample very firmly as *aethusae*.

Gall AL.

Characters of alatae as in AJ and AK. Choice offered and result of test as for AI. Sample apparently *aethusae*.

Gall AM.

One alata preserved. Chaetotaxy S.S.L., macula extensive and solid. M.T./7 absent. Rhin./V 1-3, mean 2. Negative reaction to *Aethusa*, *Torilis* and *Petroselinum*. This test perhaps failed through paucity of alatae available from the gall. No conclusions drawn.

Gall AN.

Chaetotaxy S.S.L., macula extensive and solid. M.T./7 absent. Rhin./V 0. *Heracleum* only offered; result negative. No conclusions drawn; the sample might have been *aethusae*.

9 (iv). *Conclusions from 1953 Experiments.*

The principal fact confirmed by the 1953 series of tests was the biological reality of *Sappaphis aethusae* (Börner), and its readiness to use both *Aethusa* and *Torilis* as secondary hosts, the former being on the whole slightly better from the nutritional viewpoint.

The single gall transference technique made it impossible to test more than a small number of galls, and as all the samples used were collected from a single locality some degree of uniformity in the results obtained might be expected; however, against this may be set the removal of any influence exercised on the choice made by the aphids through the presence of alatae from other gall samples.

It was observed that cultures resulting from the transference of AB, AH, AK and AL to *Torilis* showed a rather typical facies in the apterae when alive, the dorsum being rather uniformly whitish on the central area, which gave the aphids the appearance of being parasitized. This same facies had been previously noted in apterae collected from *Torilis* in the field. Since apterae reared on *Aethusa*, but

derived from these same galls, did not show this characteristic it is clearly an environmental effect associated with life on *Torilis*.

It was noticeable that nearly all the red galls collected in the spring of 1953 showed some trace of yellow mottling either at the edges or in the centre of the area of red discoloration. This may perhaps have been correlated with climatic conditions prevailing during the maturation of the galls.

10. SUMMARY OF RESULTS (1954).

The aim of the 1954 series of experiments was to elucidate as far as possible the main problem outstanding from the three previous years : the status and relationship to *crataegi* Kltb. of the form named *kunzei* by Börner (1950)). This form had proved curiously elusive in gall collections, and only one apparently reliable culture had been obtained (K.2, 1951).

In spite of the satisfactory results given by single gall transference tests in 1953 it was apparent that the small number of galls which could be tested was an important consideration against repeating this technique in 1954. The method finally adopted was the collection of as many galls as possible and their grouping for transference purposes on the basis of colour data and preliminary morphological examination of the resulting alatae. Since previous years' experiments had failed to confirm Börner's nymph colour character for aphids migrating to *Pastinaca* it was decided to proceed on the assumption that *Pastinaca* would be colonized by the alatae coming from pinkish nymphs, and having the macula broken on the intersegments.

Unfortunately the earlier part of the transference programme was made unprofitable by the onset of very cold wintry weather which produced such sluggishness in the alatae that many died without moving out of the tubes in which they were transferred to the choice cages. A further misfortune was that plants which had been collected in the rosette stage as *Pastinaca* were later found to be misidentified, and turned out to be *Apium nodiflorum*. This unfortunate error meant that transferences up to 26 May were made with *Apium nodiflorum* taking the place of *Pastinaca*. However, some slight good could result from the mistake, since *Apium nodiflorum*, which has no recorded use as a host to *Sappaphis* species, could act as a control when offered to green nymph alatae together with its congener *Apium graveolens*.

10 (i) *Gall data (tabulated)* see p. 674-5

10 (ii) *Transferences performed and results obtained (tabulated)* see p. 676

10 (iii). *Recovery of Alatae.*

For reasons of space in the insectary it was necessary to combine cultures obtained from colonizations of *Daucus* and *Pastinaca* at a very early stage, with the result that alate recoveries could not reliably be sorted into their respective classes of origin in the majority of cases. The recoveries from *Pastinaca* were in any case very few, only one alate being recovered from series DC, DD, DE, DF and DT, while the eight recovered from gall EA were in fact the same eight specimens whose morphological characters are recorded in section (i), Table IV.

A total of 86 alatae were recovered from all *Daucus* cultures. These were scored for the degree of solidity of the dorsal macula in three classes : (1) solid, (2) intermediate (i.e. with some spots or lines of weakness along intersegments) and (3) broken (i.e. with more or less complete membranous lines along intersegments 3/4, 4/5 and 5/6). Distribution by classes was :

Solid	40
Intermediate	29
Broken	17

No alatae were recovered from the reluctant colonization of *Apium graveolens* by green nymph alatae of BS, BU, BV etc.

10 (i). *Gall Data*
TABLE IV.—Tabulated data for 1954 Gall Samples.

1954 Gall Samples.

Gall	Locality	O.S. grid ref.	Gall colour	Nymph colour	Wax	Alate characters:						Macula	
						Hair length maxima (μ)			M.T. 7T		Rhin/V		
						III	3T	8T	2	1	0		Range/Mean
BA	Cambridge	436596	5	Pinkish	3-4	12	15	48	0	0	1	0-1/0.5	Nearly solid.
BB	"	452573	5	Pinkish to pink	1-2	14-16	16-18	36-43	0	1	1	0-3/1.25	Broken on 3/4.
BC	"	452573	4	Pinkish	2	13-19	14-19	22-55	0	2	6	0-4/1.5	Solid.
BD	"	452573	4	Pink	2	15-18	13-17	31-58	0	1	3	0-1/0.125	"
BE	"	452573	4	{ Greenish-grey & Ochreous, 50/50	3	{ 12	11	13-16	1	0	1	5-10/6.75	Broken.
BG	"	452573	4	{ pinkish ant. Ochr. { greenish post.	4	{ 15	16	36	0	0	1	0/0	Solid
						18	17	44	0	1	0	0/0	"
BH	"	452573	5	Greyish-pink	3	19	12	38	0	1	0	2-3/2.5	Solid.
BI	"	452573	3	Pink	2	13	12-13	26	0	0	2	0-3/1.75	"
BM	"	436596	3-4	Pinkish-grey	4	14-15	12-14	30	0	2	1	0-3/0.83	Nearly solid.
BN	"	436596	4	Pinkish- to lilac-grey	4	14-17	11-13	21-29	0	0	2	0-1/0.25	Solid.
BO	"	436596	5	Pink	3	13	14	38	0	1	0	0/0	Broken on 3/4, slight- ly on 4/5.
BR	"	436596	5	Pinkish- to lilac-lead	3	12-14	14	63-64	0	0	2	0-2/0.75	Solid.
BS	"	436596	4	Green	3	9-13	10-13	22-29	5	1	0	0-13/3.58	Broken on 3/4, sele- rite 3 v. small
BU	"	436596	4-5	"	3	10-12	12-13	20-26	1	0	1	3-6/4.25	Broken on 3/4.
BV	"	436596	3-4	"	3	9-11	9	14	0	0	2	4-5/4.33	Broken.
*BX	"	437597	4-5	Greyish-pink	3-4	14-18	14-17	46-63	0	2	1	0-4/1.0	Solid.
BY	"	437597	2-3	Pink	4	14	14-18	37-41	0	0	3	0-4/0.8	"
BZ	"	437597	3-4	"	4	13-14	14	19-63	2	0	0	1-4/2.0	Nearly solid.
CA	"	437597	4	Greyish-pink	4	12-14	14	30-36	0	1	1	0-3/1.5	"
CD	"	437597	5	Pink	4	14-16	11-13	33-37	0	1	2	0-4/2.0	Solid.
*CE	"	438598	3-4	Green	4	11-12	12	19-22	2	1	0	1-5/2.67	Broken on 3/4.
CF	"	438598	3	"	3	11-13	11-14	19	1	2	1	1-8/4.5	"
CH	"	438598	3-4	"	3	11-13	13-18	18-19	2	1	0	2-6/3.67	Slightly broken on 3/4 (and 4/5).
CI	"	438598	4	"	3-4	9-11	11-13	13-26	1	2	0	2-4/2.83	Broken on 3/4.
CJ	"	438598	4	"	3	9-12	11-13	19-20	0	2	0	2/2.0	"

CM	444587	4	Pink	3	11-14	14-18	38-44	0	0	5	0-2/0-55	Nearly solid.
CN	444587	2	"	3	12-15	14-18	27-44	2	11	11	0-4/0-33	Nearly solid to partly broken on 3/4 and 4/5.
CO	444587	4	"	4	11-14	11-18	25-29	0	7	8	0-3/0-44	Solid.
CP	444587	3	"	3	13	13	47	0	0	1	0-1/0-5	Nearly solid.
CQ	443586	3	"	3	11-13	11-14	36-52	5	9	2	0-3/1-13	Broken on 3/4, 4/5, and 5/6.
CS	443586	3-4	"	3	10-14	12-14	32-53	0	3	17	0-3/0-74	Some weakness on 3/4, 4/5.
DC	491547	4-5	"	4	11	14	37-52	0	2	0	0-2/0-5	Broken on 3/4, 4/5, and 5/6.
DD	491547	4-5	"	3	14	14	52	0	1	0	0/0	"
DE	491547	4	"	2-3	11	14	48	0	0	1	0/0	"
DF	491547	4-5	Greyish-pink	3	11-15	12-13	33-47	1	0	2	0/0	"
DG	491547	4-5	Pink	4-5	12-14	13-18	20-46	0	0	4	0-2/0-63	Weak on 3/4, 4/5.
DH	491547	4	Greyish-pink	3	13-16	18-24	38-57	0	1	2	0-1/0-17	Slightly weak on 3/4, and 4/5.
DI	491547	4-5	Pink to pinkish-grey	3	13	18	55	0	1	0	0/0	Broken on 3/4, 4/5, and 5/6.
DJ	491547	4	Dull olive-pinkish	2	18	16-32	45-55	0	0	2	0-3/1-0	1 solid, 1 broken on 3/4.
DM	491547	4	Pinkish-grey to leaden	4	13-15	12-15	43-58	1	1	4	0-4/1-08	Solid and extensive.
DN	491547	3-4	Pink to greyish-pink	4	18-21	20-29	54-57	0	0	2	0-4/1-5	Weakened on 3/4, 4/5, and 5/6.
DO	491547	4	Pink	4	20	35	45	0	1	0	0-1/0-5	Extensive and nearly solid.
DP	491547	5	Dull olive-pink	4	13-15	12-15	38-57	0	2	1	0-2/0-5	Solid or nearly so.
DQ	491547	3-4	Dusky pink	4	12-13	13-16	46-55	0	0	5	0-3/0-5	Solid and extensive.
DR	491547	3-4	Dark dusky pink	4	12-13	13-18	61-69	0	1	1	0-5/1-25	Slightly weak on 3/4 and 4/5.
DS	491547	4-5	Pink	3	11-14	11-18	48-60	0	0	5	0-3/0-4	Solid and extensive.
DT	491547	3-4	Pinkish-grey	4	12	11-13	56-59	0	1	1	0-4/1-25	Nearly solid to weak on 3/4 and 4/5.
*DU	491547	4	Pink	4	13-14	14	43-59	0	2	4	0-2/0-42	Solid and extensive.
DV	491547	5	Dull olive	4	14	12	39-42	0	0	2	0/0	V. slightly weak on 3/4.
DW	491547	5	Dull pink	4	14	14-18	40-62	0	0	2	0/0	Solid.
DY	491547	5	Pink	4	16-18	15-18	54	0	2	1	0/0	"
EA	491547	4	Greyish-pink	4	11-13	9-14	24-42	0	1	7	0/0	Nearly solid to weak on 3/4, 4/5.

* Gall with 2 fundatrices.

10 (ii). *Transferences Performed and Results Obtained.*

The following choices were offered :

Galls used	Choice offered	Result
BN and BR	<i>Apium nodiflorum</i>	—
BA, BM and BO	<i>Daucus carota</i>	±
BL	" "	—
BJ	" "	—
BG	<i>Apium nodiflorum</i>	—
BB, BC, BD, BH, and BI	<i>Heracleum sphondylium</i> <i>Daucus carota</i> <i>Apium nodiflorum</i>	— + —
BE	<i>Heracleum sphondylium</i> <i>Daucus carota</i> <i>Apium nodiflorum</i>	— — —
BS, BU, BV, CE, CF, CG, CH, CI and CJ (1st transfer, 20.v.54)	<i>Apium graveolens</i> f. <i>dulce</i> <i>Apium nodiflorum</i>	Aggregation of alatae on <i>A. graveolens</i> ; no settle- ment on <i>A. nodiflorum</i> .
Same combination (2nd transfer, 24.v.54)	<i>Apium graveolens</i> f. <i>dulce</i> <i>Apium nodiflorum</i>	± (not basal). —
BX, BY, BZ, CA and CD	<i>Heracleum sphondylium</i> <i>Daucus carota</i> <i>Apium nodiflorum</i>	— — —
CK and CL	" "	—
CM, CN, CO, CP, CQ and CS	<i>Daucus carota</i> <i>Apium nodiflorum</i>	+ —
DC, DD, DE, DF and DT	<i>Daucus carota</i> <i>Pastinaca sativa</i>	— +
DG, DM, DO, DQ, DU and DY	<i>Daucus carota</i> <i>Pastinaca sativa</i>	± +
DH, DI, DJ, DN, DP, DR, DS and DV	<i>Pastinaca sativa</i>	+
DW	<i>Heracleum sphondylium</i>	—
EA	<i>Daucus carota</i> <i>Pastinaca sativa</i>	— +

10 (iv). *Conclusions from 1954 Experiments.*

(1) Green nymphs in all cases gave rise to alatae of typical *inculta* facies. They were offered two species of *Apium*, *graveolens* and *nodiflorum*, of which the former was colonized with reluctance, settlement not being basal initially. This result agreed with observations made in the 1952 series of experiments (see p. 665).

(2) Pink nymphs with moderate to strong wax pulverulence gave rise to alatae both of the expected *crataegi* and of the expected *kunzei* types, and to individuals

intermediate between the two extremes. Both *Daucus* and *Pastinaca* were successfully colonized, but the postulated separation on the basis of the degree of break-up of the dorsal macula was very incompletely realized. Alatae with the most strongly broken macula colonized *Pastinaca* and rejected *Daucus* according to expectation; but those with an entire or less broken macula showed a tendency to prefer *Pastinaca* also when offered with *Daucus*, although *Daucus* was accepted as well.

(3) *Apium nodiflorum* was not accepted in any test, and is apparently not a possible host of any of the aphids tested.

11. GENERAL DISCUSSION.

In spite of the limitations of the experimental work described in the foregoing pages it is possible to draw from it a number of deductions about the status of the various forms of *Sappaphis* migrating from *Crataegus*. It is convenient to group these deductions under the headings of the various taxa which have been named by Börner, and to add sections on certain general considerations afterwards.

(1) *Sappaphis inculta* (Börner nec Wlk.) = *apiifolia* Theob. (Börner).

In its typical form this taxon is easily distinguishable from the other hawthorn *Sappaphis*. Observations on the 1951, 1952 and 1954 series of experiments indicate that red galls containing green nymphs almost invariably give rise in Cambridgeshire to aphids with the characters of *apiifolia sensu* Börner, and when tested against *Petroselinum crispum* and *Apium graveolens* positive results were obtained, except in two instances in 1952 (Q.1 and series T), where *Apium* was not colonized. It seems likely, however, that the green or pink colour character is not uniform in its associations with different taxa over the whole distribution range of hawthorn *Sappaphis*, since Börner (1950) ascribes green nymphs to *kunzei*, and a sample of *crataegi* Klth. collected by me in northern Italy in 1955 (see p. 000) was green in the nymphal stages on *Crataegus*.

It was noted in 1952 and 1954 that *Apium graveolens*, when colonized, was only reluctantly so as compared with *Petroselinum*, while *Apium nodiflorum* was not accepted at all (1954). Further work on the relative acceptability of parsley and celery to *apiifolia* is required for certainty, but these observations suggest that Börner's division of "*inculta*" into three subspecies has some basis in fact so far as ssp. *petroselini* is concerned, and that the common British heteroecious form belongs to this latter subspecies. The applicability of the name *apiifolia*, however, is doubtful. The true *apiifolia* Theobald is a species described from the Middle East, and also recorded (as *ferruginea-striata* Essig) from California (*vide* Stroyan, 1953). In both these areas it is apparently anholocyclic on celery and various other aromatic Umbelliferae, and on *Conium maculatum*. It differs very slightly in its morphology from the British green nymph material on *Crataegus*, although the two could be regarded as offshoots of a single stock. There is a single possible record of *apiifolia sensu stricto* in Britain (from *Conium maculatum* in Essex, F. H. Jacob leg.). Börner (1952) records *Conium* as an alternative host of his subspecies *nudicaulium* living on *Levisticum*, but this point is probably not significant since *Conium* seems to be an instance of the "reserve host" phenomenon which will be discussed later. What is of more importance is that Börner ascribes to *apiifolia* a primary host association with *Crataegus*, which the typical (i.e. North African) form may not have. All the British material so far tested has shown a preference for *Petroselinum* and a comparatively weak inclination to accept *Apium*; it should therefore be known as *petroselini* Börner, and henceforth will be so called in this discussion. Whether a truly holocyclic taxon migrating between *Crataegus* and *Apium* (i.e. preferring *Apium* to *Petroselinum*) exists in Europe, or whether Börner was misled by the sometimes rather easy transference of *petroselini* to celery, is not known with certainty.

yet. Whatever the answer to this, it seems advisable to restrict the name *apiifolia* Theob. to the anholocyclic Mediterranean celery aphid.

Although, as stated above, the typical *petroselini* facies is unmistakable, being based on a combination of six characters whose ranges of variation differ from those of the other short-haired forms on hawthorn, complications exist which make it necessary to consider the status of *petroselini* at greater length. From time to time during the course of the experimental programme described above gall samples have been collected whose alate emigrants exhibit to a greater or lesser extent some of the characters of typical *petroselini* without the others. These samples do not agree closely with any population so far detected on a secondary host in the field. As examples of such galls may be cited the following :

1951 : C.2, E.2, 3, 7, F.2, G.5, 7, 10, M.3, 5, 7, 10.

1952 : Q.6, T.2, 4, 8, 9, R.3.

1953 : AE.

1954 : BV, BW.

It is noticeable that in most of these instances the samples with low-grade expression of *petroselini* characters were collected from the same hawthorn bush or hedge as other samples which yielded typical *petroselini*, or aphids with at most lowered expression of a single character : e.g. C.4, G.1, Q.7, T.10, BS. In the event of lowered expression of a single character sample size may frequently offer a reasonable explanation, e.g. Q.7 is represented by a single alata, the absence from which of the marginal tubercles of the seventh tergite is of no significance when balanced against the expression of other *petroselini* characters. But where several of the characters typical of *petroselini* show a similar and simultaneous lowering of expression it is necessary to ask the question whether these samples represent part of the normal *petroselini* range of variation or should be ascribed to one or more of the other short-haired taxa, or accounted for in some other way.

To test this a system of arbitrary scoring was devised covering the five principal characters common to typical samples of *petroselini*. While this system was calculated to show up the differences between *petroselini* and the other short-haired taxa it could not distinguish between the latter ; and its use was therefore restricted to trying to detect any bimodality within the material showing *petroselini* characters. Further, since the scoring system was arbitrary it took no account of any weighting which might be theoretically desirable between characters to give the truest picture of their degrees of correlation with one another.

A total of 42 gall samples showing possible or definite affinity with *petroselini* was scored on this basis, the scoring plan being as follows :

1. Marginal tubercles on seventh abdominal tergite, expressed as a fraction of the total possible (i.e. $2n$ for a sample of n aphids) to a base of 10 and to the nearest whole number, thus giving a score range of 0 to 10. Scores were then halved to the nearest whole number (halves counting to the next higher integer) giving a final score of 0 to 5.

2. Mean hair length maximum for eighth abdominal tergite, in six arbitrary classes from $10\ \mu$ to more than $60\ \mu$, giving a score range of 0 to 5.

3. Mean number of secondary rhinaria on ant. V, per antenna, to the nearest integer.

4. Solidity or degree of break-up of dorsal macula, scored from 0 (solid) to 2 (strongly broken), and doubled to increase scoring power.

5. Nymph colour, from pink to green, scored on a scale from 1 (pink) to 4 (green).

The results of this scoring technique show clearly that it is possible to collect gall samples showing a complete series of intergradation between typical *petroselini* and the other three short-haired forms, whether scoring is confined to a single character,

to selected pairs of characters or applied to all five simultaneously. The scores do show a marked bimodality in their distribution, and this bimodality gives a rough means of determining how many of the 42 samples examined lie within the limits of true *petroselini*, and, following from this, some idea of the degree of exclusiveness with which any one of the postulated characters of *petroselini* is associated with it.

From inspection of the distribution curve (Fig. 1) it is apparent that samples with scores of 14 and upwards may be regarded as lying within the range of variation of *petroselini*. This range includes 21 of the 42 samples examined, and the distribution of this group of samples is normal in form.

TABLE V.—Scoring for samples exhibiting one or more characters of *S. petroselini* (Börner).

Sample	M.T./7T	H.L./8T	Rhin./V	Macula	Nymph colour	Total score
P.4	5	4	6	4	4	23
CR	4	5	5	4	4	22
P.3	4	4	5	4	4	21
BS	5	4	4	4	4	21
CF	3	5	5	4	4	21
C.4	4	5	5	4	2	20
T.10	3	4	6	4	3	20
CE	4	5	3	4	4	20
CI	4	5	3	4	4	20
G.1	3	4	4	4	4	19
BU	3	4	4	4	4	19
CH	4	5	4	2	4	19
AE	4	4	6	2	2	18
T.5	3	4	6	2	3	18
Q.7	0	5	7	2	4	18
T.1	1	5	5	4	3	18
CJ	3	5	2	4	4	18
BV	0	5	4	4	4	17
Q.1	2	4	7	0	3	16
C.2	0	4	5	4	2	15
Q.2	3	2	1	4	4	14
T.8	2	2	7	0	2	13
T.4	0	5	3	2	3	13
BW	1	3	4	0	4	12
E.3	3	3	2	2	2	12
T.9	0	0	8	2	2	12
R.3	4	1	0	4	2	11
E.7	2	2	1	4	2	11
T.2	1	2	6	0	2	11
M.10	0	2	2	2	4	10
E.2	1	4	1	2	2	10
G.7	2	3	2	2	1	10
Q.6	2	2	1	2	2	9
P.1	0	2	2	4	1	9
M.5	0	1	3	0	4	8
G.5	2	2	1	2	1	8
M.3	1	2	0	4	1	8
G.10	0	3	1	2	2	8
F.2	2	1	1	0	1	5
M.7	0	0	1	0	4	5
P.2	0	3	0	0	1	4
P.5	1	1	0	0	1	3

The lower peak of the distribution is somewhat skew, which reflects the fact that the samples scored were selected for characters typical of the higher scoring group, and were not a random sample of the non-*petroselini* population. The limits of the

petroselini taxon as determined by this method do not conflict in any way with the biological evidence available.

The status of the 21 samples lying below the 14 score level is not apparent from inspection of the distribution. Since no samples clearly belonging to other short-haired taxa were included in the scoring test it is not possible to determine whether these lower-scoring samples form part of the tail of the distribution for these other taxa; and since the other short-haired forms are not differentiated on the basis of the five characters used, the residual problem cannot be solved by extension of the same scoring method to all the other short-haired experimental samples.

However, in this connection the following points may be kept in mind :

(i) The gall series T (1952), which includes three samples of *petroselini* proper (T.1, 5, 10) and four samples lying on the lower part of the distribution (T.2, 4, 8, 9), was offered a complete host range including *Daucus*, *Pastinaca* and *Aethusa*. If the four lower-scoring samples in fact belonged to any of the other short-haired taxa some colonization of one or another of the three named hosts would be expected.

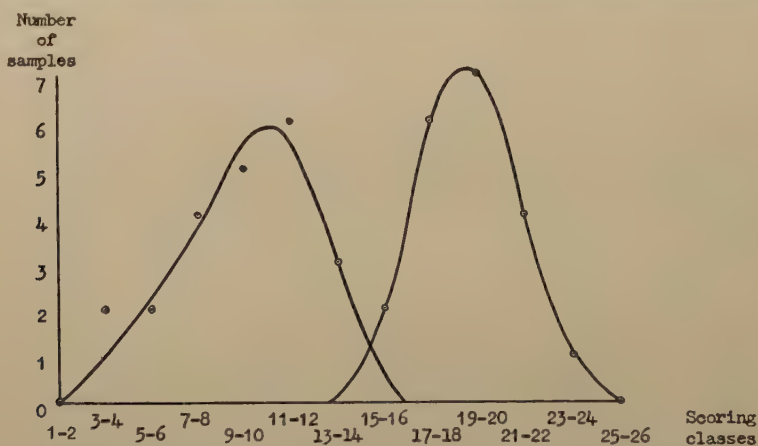


FIG. 1.—Frequency distribution of scores for samples with one or more characters of *petroselini* (see Table V)

Actually no such colonization resulted, except for a small colony formed on *Aethusa*, which as noted above (p. 669) was descended from three alatae, two of which were *petroselini* and gave rise to typical apterous *petroselini* progeny, while the third agreed most closely with the alatae derived from T.3 or T.6, neither of which showed any *petroselini* character tendencies; this last was presumably *aethusae* Börner. Bearing in mind the fact that the conditions of the experiment were such as to minimize host specificity (see p. 650) one must conclude that the alatae of T.2, 4, 8 and 9 were not positively responsive to the hosts of *crataegi*, *kunzei* or *aethusae*. There remains the possibility that these four samples were in part representative of *inculta* Wlk. (Börner) *sensu stricto*. This is negated by the fact that *Apium* was rejected in this series of tests. There is thus no evidence for supposing that the samples T.2, 4, 8 and 9 belong to any of the other short-haired taxa used by Börner. The implication of this will be discussed in later paragraphs.

(ii) Out of 21 samples lying outside the range of *petroselini* but exhibiting characters similar to it in some respects, no fewer than 14 (E.2, 3, 7, G.5, 7, 10, P.1, 2, 5, Q.6, T.2, 4, 8, 9) were collected from the same bush or hedge as samples of (a) true *petroselini* and (b) at least one other short-haired taxon of the *crataegi* group. Of the remaining seven samples three (F.2, R.3, BW) were collected from bushes within 100 yards of known sites of such mixed infestations, and it may be inferred that the collection of larger numbers of galls could probably have revealed a similar state of

affairs. No significant information is available from the collection data of M.3, 5, 7 and 10.

(iii) A rough test for any difference in the degree of exclusiveness with which the five characters used are associated with *petroselini* has been obtained from the frequency distributions of their scores (a) within the samples referred to true *petroselini*

1. Percentage expression of marginal tubercles on 7th tergite.

Score Group	Classes					
	0 (0%)	1 (10-20%)	2 (30-40%)	3 (50-60%)	4 (70-80%)	5 (90-100%)
(a)	3	1	1	7	7	2
(b)	8	5	6	1	1	0

and (b) within the group of lower-scoring samples. In each case the frequency range is divided at the class which most closely approaches the position where half of the total population lies to both left and right of the dividing line. The resulting distributions are as follows :

In this case it is seen that the three highest classes (with 50-100 per cent expression) contain 76 per cent of true *petroselini* samples but only 10 per cent of the lower-scoring samples. It should be noted that this character is of all the five used the least accurate for small samples, being based on a variate with only three possible values in any specimen, all of which are found in varying proportions in any given taxon (character 4 has only three possible scores, but each of these covers a certain range of variation, and the range of any taxon is restricted to a part of the total range, which makes the character relatively less sensitive to sampling error in small samples).

2. Hair length maxima on eighth tergite.

Score Group	Classes					
	0 (> 60 μ)	1 (51-60 μ)	2 (41-50 μ)	3 (31-40 μ)	4 (21-30 μ)	5 (10-20 μ)
(a)	0	0	1	0	10	10
(b)	2	4	8	5	1	1

Here the highest two classes (mean hair length maximum less than 31 μ) contain 95 per cent of true *petroselini* against 10 per cent of the lower-scoring samples.

3. Mean number of secondary rhinaria on ant. V.

Score Group	Classes								
	0	1	2	3	4	5	6	7	8
(a)	0	1	1	2	5	6	4	2	0
(b)	4	7	4	2	1	0	1	1	1

The highest five classes contain 81 per cent of true *petroselini* against 19 per cent of the lower scoring samples.

4. Break-up of dorsal macula.

Score Group	Classes		
	0 (solid)	2 (slightly weak)	4 (broken)
(a)	1	4	16
(b)	7	9	5

The highest class contains 76 per cent of *petroselini* to 24 per cent of lower-scoring samples. Here it should be noted that break-up of the macula, though on a slightly different pattern, appears also to be characteristic of *kunzei* and of undersized specimens of other taxa.

5. Colour of nymphs in galls.

Score Group	Classes			
	1 (pink to pinkish)	2 (pinkish-grey to lilac-grey)	3 (pure grey to (greenish-grey)	4 (greenish to green)
(a)	0	3	4	14
(b)	7	9	1	4

The two highest classes contain 86 per cent of *petroselini* to 24 per cent of lower-scoring samples.

If now the partition of the higher scoring half of each distribution between *petroselini* and non-*petroselini* samples is compared with a table of 5 per cent fiducial sampling limits it appears that the five characters do not differ significantly in the degree of closeness of their association with *petroselini*; this supports the validity of the scoring method as a means of diagnosing the limits of *petroselini*.

(iv) It has been explained elsewhere (Stroyan, 1955) that the relationship of body length to the ratios Body length/Antennal flagellum length and Processus terminalis/Base of VIth antennal joint, when plotted for apterae of *petroselini* (referred to as *apiifolia* Theob.), exhibits slight differences from the same relationships in apterae of the other short-haired *Sappaphis* on hawthorn (*crataegi* Kltb. *sensu latiori*); the latter apparently form parts of a single continuous range of variation, though with different frequency distributions. The interspersing of points on the scatter diagrams is, however, such that it is not possible to make use of these relationships for taxonomic purposes. Apterae of *petroselini* collected from secondary hosts in the field, on the other hand, do exhibit a high degree of expression of characters 1 and 2 in the foregoing analysis, and it is on these characters that the recognition of apterous *petroselini* chiefly rests. No population of apterae has yet been recorded either in the field or in experimental cultures whose characters agree in detail with those of the intermediate alatae comprising the lower part of the scoring range in the analysis. This point is of importance, and will be referred to again later.

(2) *Sappaphis crataegi* (Kltb.) and *S. kunzei* (Börner).

The evidence accumulated during the experimental work of 1951-54 clearly indicates that British *Sappaphis* infesting parsnip and carrot are not separable by Börner's nymph colour character (Börner, 1950). It is of course possible that this

character is useful in separating material of these two taxa in Central Europe (see p. 692) ; but in such a case the question must be posed whether in fact the British parsnip aphid constitutes a third separate taxon not identical with *kunzei* Börner. This point need not be explored here, since the objective is to discuss the status rather than the nomenclature of the British hawthorn *Sappaphis*.

Examination of wild-collected spring migrants from parsnip and carrot initially suggested that there was a distinction between *crataegi* and *kunzei* in the extent to which the dorsal macula of the alatae was broken up along the intersegments. It must be stressed again that this break-up is not a character which could be exclusive to *kunzei*, since it occurs in small hunger forms of a number of *Sappaphis* species, as well as in typical material of *S. hirsutissima* (Börner), *S. palaestinensis* H. R. L. and *S. petroselini* (Börner). However, it seemed that it would be useful to try this character as an indicator of the probable identity of short-haired migrants with *kunzei*.

In the event hopes of obtaining a simple separation of *crataegi* and *kunzei* on this character were not realized, and it became obvious that predictions of identity from examination of the macula in living alatae were unreliable. The results of the 1954 experiments have already been summarized ; and it must be recorded that an extensive and detailed re-examination of wild-collected alatae from *Pastinaca* indicated that the degree of separation given by the broken macula had been initially over-estimated.

In spite of this it seemed likely that an examination of the distribution of this character would be of value, and a scoring range from 0 to 5 was therefore devised for the varying degrees of break-up of the macula observed in the material, 0 representing the completely solid condition and 5 the most strongly broken, in which all the segmental components of the macula are clearly separated by more or less continuous membranous lines on the intersegments. All available material was then scored as accurately as possible. The frequency distribution for the whole population (287 alatae) was :

Score	0	1	2	3	4	5
Percentage individuals	16.0	26.1	20.6	26.5	7.7	3.1

This distribution is clearly bimodal, with peaks at scores 1 and 3. If now the total population is divided into alatae collected or recovered from *Daucus* and *Pastinaca* respectively, the frequency distributions are :

Score	0	1	2	3	4	5
Percentage from <i>Daucus</i>	26.9	37.2	21.4	12.4	2.1	0
Percentage from <i>Pas- tinaca</i>	4.9	14.8	19.7	40.9	13.4	6.3

This second distribution pattern shows unmistakably that there is a pronounced positive correlation between break-up of the macula and selection of *Pastinaca* as secondary host, but that the overlap is such as to make the character taxonomically of little value. This could be due to either or both of two factors : (a) a morphological intergrading between two forms with mutually exclusive host preferences, or (b) a certain degree of ambivalence in host selection in two morphologically distinct taxa. Available evidence suggests that both factors play some part in obscuring the separation of *crataegi* from *kunzei*, as will be seen from the following observations :

(i) Gall sample EA, a clonal sample which selected *Pastinaca* and rejected *Daucus* in a single-gall transference test, and is therefore to be regarded as biologically pure *kunzei*, was compared with gall sample AA, a similarly clonal sample which selected *Daucus* and rejected *Pastinaca* in a similar test, and should therefore be biologically pure *crataegi*. Nine alatae were available from each clone, and the distributions of their scores for break-up of the macula were :

Score	0	1	2	3	4	5
Gall EA	0	1	5	3	0	0
Gall AA	0	1	2	6	0	0

The range of variation is the same in both samples, and the distribution is not significantly different bearing in mind the smallness of the samples. This observation favours factor (a) in the previous paragraph.

(ii) In April 1955 while in Northern Italy the writer collected a gall sample of *Sappaphis* from a *Crataegus* bush in the Botanic Garden of Parma University. On returning to England the migrants derived from these galls were offered *Pastinaca* and *Daucus* in a free choice test. Both hosts were colonized, the latter much more strongly than the former. Cultures derived from the transference were bred on until the appearance of the midsummer alate generation. When the two alate generations of these aphids were scored for the break-up of the dorsal macula the following distribution was obtained :

Score	0	1	2	3	4	5
Spring migr. percentage	13.9	72.2	13.9	0	0	0
Midsummer al. percentage	7.4	43.0	41.3	8.3	0	0

The two distributions are completely normal and unimodal, indicating that the material was homogeneous for the macula character ; the relative strengths of colonization of *Daucus* and *Pastinaca* together with the low scoring range in the above table indicate that the taxon involved was *crataegi* Kltb. ; while the rather ready acceptance of *Pastinaca* shows that some ambivalence in host preference was present, though perhaps reinforced by the fact that the season in Italy was several weeks in advance of that in Britain, so that the alatae were encountering host plants in a more juvenile condition than would have been the case in nature. This last point may be of some importance in explaining host selection anomalies, and will be returned to again in a later part of the discussion. It is enough here to say that this observation appears to lend support to factor (b) mentioned on p. 683.

A further point emerging from this last frequency distribution is that the midsummer alatae show a wider range of variation in the form of the macula than do the spring migrants. This is probably correlated in the case of *crataegi* with the non-specific phenomenon of break-up of the macula in undersized specimens, most of the midsummer alatae being small in size. The converse phenomenon in *kunzei*, which on this basis would be expected to be absent or at least less pronounced, is in fact less pronounced in the recoveries from *Pastinaca* after the 1954 series of experiments. Thus, although in both populations the variance of the midsummer alatae is twice that of the spring migrants, in the Italian *crataegi* the difference between the means for the two generations is about one-third of the sum of the standard deviations, while in the 1954 *Pastinaca* material it is only one-seventh of the sum of the standard deviations.

Attempts to find further characters offering appreciable degrees of separation (i.e. of a magnitude which would be taxonomically useful) between *crataegi* and *kunzei* have been unsuccessful. A comparison was made between the mean hair length maxima on the eighth tergite for 1954 recoveries from *Daucus* and *Pastinaca*. The result was :

	<i>Daucus</i> (13 alatae)	<i>Pastinaca</i> (28 alatae)
Mean maximum	36 μ	41 μ
Standard deviation	8.5 μ	11 μ

These differences are clearly not significant, the difference between the means being only just over one-quarter of the sum of the standard deviations.

There does appear to be a very slight degree of separation between the two forms on the mean number of secondary rhinaria occurring on the fifth antennal joint in spring migrants ; but as the distribution is of truncated form with the mode at 0 in both cases this is not useful taxonomically. Using all available spring migrant material of both taxa the results given are :

	Number of antennae examined	Rhinaria counted	Range of sample means (per antenna)	Overall mean
<i>kunzei</i>	130	18	0.0-0.25	0.14
<i>crataegi</i>	130	69	0.22-1.50	0.53

There is also a small difference in the overall distribution of marginal tubercles on the seventh abdominal tergite in the two taxa. Thus wild populations of *crataegi* and *kunzei* had paired or unpaired tubercles present in 10 per cent and 30 per cent respectively of the available apterae, while the comparable figures for experimental apterae were 9 per cent and 27 per cent respectively. This character cannot be applied to single specimens, however ; and in both forms the range of percentage distributions found in individual samples varied too widely for the percentage to be useful for separating small lots of specimens.

The only conclusion possible from the available data is that Börner's taxa *crataegi* Kltb. (s. str.) and *kunzei* Börner are insufficiently differentiated either morphologically or biologically to be treated as good species, although there is sufficient correlation between morphological and biological characters to indicate the existence of two incipient subspecies, that on *Pastinaca* having a higher expression of the break-up of the macula, a higher incidence of marginal tubercles on the seventh tergite and a less frequent incidence of rhinaria on the fifth antennal joint in alatae than that on *Daucus*. The only character given by Börner for recognition of *kunzei* (green nymphs in the spring galls on *Crataegus*) does not hold at all for the British material examined, so that *kunzei* is virtually a *nomen nudum*, unless it was actually based on a second, distinct taxon not represented in British collections as yet.

Following from these conclusions it might be expected that *crataegi* and *kunzei*, which are ecologically sympatric on *Crataegus* where sexual reproduction occurs, should exhibit a certain amount of interfertility, with the consequent presence in spring populations of forms with some intermediate hybrid characters. Such forms in addition to complicating the morphological picture might also be expected to be less well adapted to host selection between *Daucus* and *Pastinaca* than pure bred material of either taxon.

Börner (1952, p. 15) states categorically that males of *Yezabura* (his name for the group under discussion) will identify oviparae of their own species from among mixed groups sitting on the same hawthorn leaf. His grounds for this statement are not given. Preliminary experiments by the writer in October 1954 showed that spontaneous copulation between male *crataegi* from *Daucus* and oviparae born of gynoparae from *Pastinaca* will occur in the absence of other oviparae, and that ova are laid which appear to be fertile (turning black normally and retaining their shape for a matter of months). Unfortunately it was impossible to obtain enough ova to overwinter any successfully, and the question still awaits final settlement, whether such irregular unions can be produced in mixed populations. However, if cross-copulation can occur in the absence of oviparae belonging to the same taxon as the males concerned it is possible to envisage numerous occasions when such crossing would take place in the field. The pre-copulation behaviour of aphids is not complex, consisting of a waving of the hind tibiae (bearing glands of a probably olfactory nature) by the oviparae and an excited but generalized reaction by the male when within a centimetre or two of the ovipara. No behavioural barrier seems likely between these very closely related forms of *Sappaphis*, and no reluctance to copulate was observed in the oviparae used in the experiment referred to above.

(3) *Sappaphis aethusae* (Börner).

This taxon was the commonest hawthorn *Sappaphis* among the 1951 and 1953 experimental collections in the Cambridge area. Its biological characters are well-marked and consistent. *Aethusa cynapium* and *Torilis japonica* are readily colonized by spring migrants; *Daucus*, *Pastinaca*, *Heracleum*, *Petroselinum*, *Angelica* and *Choerophyllum* are refused. *Smyrniolum olusatrum* is apparently a possible host, both in the field and in experimental transferences. To judge from the experimental results, *aethusae* is more effectively isolated biologically from *crataegi* and *kunzei* than the two latter are from each other. In no instance has a sample of *aethusae* been found to show any readiness to accept *Daucus* or *Pastinaca*, and in only one case has a sample of *crataegi* (AA) reluctantly and with difficulty colonized *Aethusa* and *Torilis*.

In contrast to this biological homogeneity it must be recorded that morphological criteria for separation of *aethusae* from *crataegi* and *kunzei* are hard to find. It has been shown elsewhere (Stroyan, 1955) that Börner's characters for separation of *aethusae* are not valid, but that there is in fact a slight degree of separation between the three taxa in their relative tendencies to produce alatiform apterae; this is reflected in the degree of development of the abdominal sclerotic pattern and the length relations of the body, antennal flagellum, processus terminalis and basal part of antennal joint VI. Comparable degrees of alatiform expression in the three taxa are morphologically inseparable by any simple criterion.

The 1951 series of experiments suggested that a salient feature of the spring migrants of *aethusae* is the very extensive and solid dorsal macula on the abdomen. This was again noted in the 1953 series. A quantitative evaluation of this character has been attempted, using (a) the scoring range for solidity or break-up of the macula devised for comparing *kunzei* with *crataegi*, but with the scoring reversed, i.e. score 0 for maximum break-up and 5 for maximum solidity, and (b) a scoring range from 0 to 2 for actual size of the pigmented area. This latter score is based on the width of the membranous pleural area lying between the edges of the macula and the marginal sclerites of abdominal segments 3-5. Where this is consistently wider than the siphuncular diameter at the base a score of 0 is awarded; where consistently narrower a score of 2; and in specimens where both conditions are present on one or more segments between 3 and 5 a score of 1. Application of this scoring scale is not easy; in mounting, the membranous pleural area is frequently made inconspicuous by folding of the cuticle; and it is necessary to ignore the pleural intersegmental

sclerites and pay attention only to the lateral terminations of the segmental tergal components of the macula.

The results of applying these scoring methods to all the available spring migrant material which can be unequivocally called *aethusae* on biological grounds is shown in tabular form in conjunction with the figures for the spring migrants of *crataegi* and *kunzei*. (N.B.—The fact that these latter distributions differ slightly in percentage, though not in modality, from the previously shown distributions of the same character is due to the fact that only spring migrant material is used in the present table, while that given in the discussion of *crataegi* and *kunzei* was based on all available material.)

In view of the fact previously referred to that a reduction in size and solidity of the macula is characteristic of small hunger forms of *Sappaphis* it was felt advisable to test the possibility that the above distributions were correlated with the size of the

(a) Distribution of scores for solidity of macula.

Score Taxon	5	4	3	2	1	0	Number of specimens
<i>aethusae</i> (% individuals)	90.1	7.4	2.5	0	0	0	81
<i>crataegi</i> (% individuals)	29.8	36.6	21.4	10.7	1.5	0	133
<i>kunzei</i> (% individuals)	6.5	16.9	18.2	35.0	14.3	9.1	77

(b) Scored for area of pigmentation.

Score Taxon	0	1	2
<i>aethusae</i> (% individuals)	2.5	6.2	91.3
<i>crataegi</i> (% individuals)	34.6	46.6	18.8
<i>kunzei</i> (% individuals)	28.6	35.0	36.4

aphids. To test this a random sample of 20 specimens of each taxon was drawn from the material used in the comparison, and the body lengths measured. The resulting data were :

Taxon	Length range (mm.)	Mean length (mm.)	Standard deviation
<i>aethusae</i>	1.70-2.32	2.00	0.18
<i>crataegi</i>	1.77-2.45	2.11	0.19
<i>kunzei</i>	1.68-2.36	2.07	0.22

The differences between the mean body lengths of these samples are not significant. In so far as differences do exist it is *aethusae*, whose scoring for solidity and area of the macula is highest, which has the smallest size range and mean size. It may therefore be assumed that the differences in distribution revealed by the scoring are real differences and not correlated with absolute size.

The incidence of secondary rhinaria on the fifth antennal joint in spring migrants of *aethusae* lies between the figures previously quoted for *crataegi* and *kunzei*. The data for *aethusae* are :

Number of antennae examined	Number of rhinaria counted	Range of sample means per ant.	Overall mean
225	73	0-1.50	0.32

This character is not taxonomically useful.

(It should be noted here that the application of the names *aethusae*, *crataegi* and *kunzei* to collections of specimens in the preceding paragraphs is based on the assumption of complete reliability in the results of free choice transference tests. This is obviously an approximation, the alternative to which is the assumption of similar infallibility in diagnosis from morphological characters. It is clear that in the case of these three taxa such an assumption will not fit the biological evidence ; and as the latter is relatively free from the subjective element present in any morphological assessment it has been preferred for this reason, rather than for any inherent superiority of biological over morphological characters. The process of unravelling a complex situation such as the present one proceeds essentially by pairs of approximations, from morphological and biological standpoints, followed by syntheses aimed at reducing areas of conflict to a minimum.)

The available evidence points to a rather more distinct status for *aethusae* than for its close relatives *crataegi* and *kunzei*. Biologically *aethusae* is well characterized and apparently does not overlap appreciably with the other two taxa. It may be observed that *Aethusa cynapium* is a plant of a widely different biotope from *Daucus* and *Pastinaca*, both of which as wild plants are characteristic of calcareous grassland, downs, sea cliffs and roadsides, while *Aethusa* is a short-lived weed of cultivated land, particularly gardens. The alternative secondary host of *aethusae*, *Torilis japonica*, is mainly a hedgerow plant which offers the aphids an alternative biotope in the event of a local absence or suppression of *Aethusa* (e.g. by clean cultivation or reversion of cultivated land to grass).

Morphologically there is little to separate *aethusae* from *crataegi* and *kunzei*, apart from the rather consistently large and dense dorsal macula of the alatae and the prevalence of low grade alatiform characters in the apterae. The very high percentage score for *aethusae* in the highest distribution classes for solidity and area of the macula suggest a greater homogeneity for the population of *aethusae* than for *crataegi* and *kunzei* ; but this is probably apparent rather than real, since (a) the biological evidence is more clear-cut than is the case between the two latter forms,

the apparent spread of the frequency distribution of which is probably due partly to this; and (b) the distributions are of truncate form in *aethusae*, so that the modal class contains what would otherwise be the lower half of the distribution curve.*

Taxonomically it is not practicable to regard *S. aethusae* as more than subspecifically distinct from *crataegi* and *kunzei*. The most satisfactory solution to the problem from the present evidence is to regard the two latter taxa as biological races of *S. crataegi* (Kltb.), *sensu stricto*, and to place *S. aethusae* (Börner) as a subspecies, morphologically separable by means of the characters referred to in the foregoing paragraphs when a fair quantity of material is available for examination.

(4) *Sappaphis lauberti* (Börner) and *S. angelicae* (Koch).

As noted in the preliminary (1951) conclusions, both these species are well-defined entities. Field collections originally suggested that alatae of *lauberti* should be separable from those of *angelicae* by the absence or extreme paucity of secondary rhinaria on the fifth antennal joint. This gives a very clear separation between wild collected alatae from secondary hosts at midsummer. The examination of experimental cultures and recoveries after transference tests shows a broadly similar picture, although it becomes clear that populations biologically referable to *lauberti* may be found with a fairly regular incidence of several rhinaria on joint V, particularly among spring migrant populations and gynoparae. Low figures for rhinaria on V in *angelicae* are relatively rarer. Details of rhinarial counts for joint V in all available alate material of both species are shown in the accompanying table.

TABLE VI.—Rhinarial numbers on V in *S. lauberti* and *S. angelicae*.

	Per specimen			Number of aphids	Number of samples
	Range	Mean no.	S.D.		
Spring migrants:					
<i>lauberti</i> (wild)	0-1	0.25	0.45	16	4
" (exptal.)	0-9	2.32	2.47	111	6
<i>angelicae</i> (exptal.)	6-30	15.72	6.56	25	4
Midsummer:					
<i>lauberti</i> (wild)	0-3	0.16	0.59	141	9
" (exptal.)	0-7	1.00	2.22	16	3
<i>angelicae</i> (wild)	8-21	12.00	3.24	13	1
" (exptal.)	2-23	9.59	6.26	17	2
Gynoparae:					
<i>lauberti</i> (wild)	0-6	2.92	1.78	12	2
<i>angelicae</i> (wild)	0-21	9.68	4.47	65	3

Biologically the two species are clearly distinct, and although in the 1951 transference tests a small number of alatae were recovered from the unexpected host (i.e. *lauberti* from *Angelica* and *angelicae* from *Heracleum*) no successful colonization of either host by the unexpected species of aphid was recorded. Some degree of spatial isolation in nature between populations of the two taxa might be expected from the different biotopes of the two host plants (*Angelica* in marshes or wet ditches, *Heracleum* on road verges and in relatively drier situations); but this is by no means complete, for *Heracleum* is of such widespread occurrence that the two plants may frequently be found growing in the same localities, for example where a ditch runs beside a road with grassy verges.

* The distribution is of course only apparently truncate, owing to the scoring method used and the size of the frequency classes.

Börner's hair apex character for separating apterae is not a very satisfactory one for practical purposes, since not infrequently some or all of the dorsal hairs of aphids colonizing *Heracleum* are of the type usually associated with *angelicae*. However, in typical material there is a slight difference in the character of the spinal hair apices of the two species, as may be seen by attempting to measure the exact lengths of these hairs. In *lauberti* the apex is produced into a very fine terminal filament, and there is often considerable difficulty in deciding where the exact end lies; in *angelicae* the acute but abruptly marked point can be placed with much greater ease and exactitude. Certain clones have occurred in the experimental series whose dorsal hairs are not only of the *angelicae* type but also shorter than in typical *lauberti*; notwithstanding these aphids have colonized *Heracleum* and produced alatae of the *lauberti* antennal type. In the field similar populations have on two separate occasions been found on *Pastinaca*. Further reference to these anomalous populations will be made later in the discussion.

(5) *Sappaphis ranunculi* (Kltb.).

This species is so distinct from the other species under consideration that no further comment is required on it. No difficulty has ever been experienced in predicting colonization of *Ranunculus* from spring galls on *Crataegus*. It appears that the only feature which *ranunculi* has in common with the other species living on *Crataegus* is the primary host association itself. It has been suggested elsewhere (Stroyan, 1957) that this may have been acquired by *ranunculi* at a different time from that at which the other hawthorn *Sappaphis* became associated with their primary host.

(6) *General Considerations.*

The discussion hitherto has been concerned with presenting a picture of the degree of separation found between the taxa of the *Sappaphis* complex associated with *Crataegus*. In order to reach a more comprehensive idea of the structure of this complex as a whole an examination must be made, so far as the available data allow, of the relative values of the characters used and the degree of variability to be regarded as normal within each taxon.

(6a) *Biological Characters.*

Since biological evidence has been largely used to confirm or deny the validity of morphological conclusions, a short consideration of the theoretical value of such evidence is not out of place here. In normally reproducing animals which are specifically associated with a single host, or in aphids which are holocyclic on a single host, such evidence will tend to have a status of particular value, since a change in host association, however produced (i.e. whether by mutation or by conditioning), will play a fundamental part in producing isolation between populations, and thus creating the conditions necessary for morphological divergence and speciation. In aphids with a cycle divided between a primary and a secondary host, however, such evidence when derived from choices of secondary host may not have this special status, except in so far as the secondary hosts are themselves allopatric. This is because isolation to be effective must exist at the time when sexual reproduction takes place, i.e. on the primary host. Thus in a group such as the hawthorn *Sappaphis* complex the degree of lability in secondary host preference is not necessarily an indication of the degree of isolation between populations, and should in the first place be treated as having the same order of significance as any other variable character, and not as being in any way causally related to such other variables. This point seems rather often to be overlooked by workers who regard transference experiments of the type used here as having greater taxonomic value than purely morphological criteria. The two approaches are clearly complementary to one another but in cases of conflict it should not be automatically assumed that host preference

anomalies invalidate apparently well-founded morphological conclusions. (See section 12 : Conclusions p. 708.)

In fact such host preference anomalies are of not infrequent occurrence both in wild and experimental populations of *Sappaphis*. It appears, however, that certain abnormal choices are more frequently made than others, and that certain taxa show a greater readiness than others to transgress the bounds of their normal secondary host relationship. Where a certain anomalous host choice is of relatively frequent and regular occurrence I have here and elsewhere made use of the term "reserve host" to describe the host plant anomalously colonized. This concept is not capable of rigid definition, since it obviously shades off at one end into the purely freak category and at the other end into normal polyphagy; but it serves a certain useful purpose by helping the recognition of the fact that host associations in these aphids are essentially non-rigid, and that anomalous host colonizations are not to be regarded as infractions of a natural law which must be explained away. As examples of reserve hosts may be mentioned *Conium maculatum*, which serves as an occasional host to *Sappaphis lauberti* and *S. apiifolia*; *Smyrnium olusatrum* which can be colonized by *S. lauberti*, *S. crataegi* (s. lat.) and *S. petroselini*; and *Pastinaca sativa*, which in addition to being the normal host of *S. kunzei* and the monoecious *S. bononii* (H. R. L.) is not infrequently colonized by *S. lauberti* and may be accepted, at least in experimental conditions, by *S. crataegi* (s. str.). It seems not unlikely also that *Apium graveolens* may be regarded with some justification as a reserve host of *S. petroselini*.

Sappaphis crataegi (Kltb.), as is perhaps natural in a taxon which is still probably actively evolving, seems to exhibit a greater plasticity in its host preferences than the other defined taxa of the group. In addition to the instances mentioned above material has also been seen from *Anthriscus sylvestris* and *Myrrhis odorata*. Börner (1950) has given the first of these hosts a separate named subspecies of *crataegi* (ssp. *anthrisci*), and has also erected a subspecies for material from *Aegopodium podagraria* (ssp. *aegopodii*). In 1952, however, he states that the latter has only been obtained by him in transference experiments in 1949, and has not been recorded in the field. While positive evidence is lacking at present it seems not unlikely that these two subspecies erected by Börner are based on examples of anomalous or reserve host colonization. It is perhaps worth while to recall that in the 1951 series of experiments carried out by the writer a colony was obtained on *Rumex obtusifolius* whose characters served to determine the aphids as *S. lauberti*, while *Heracleum*, which was also offered, was not colonized. Needless to say no collection of *lauberti* has ever been made from *Rumex* in the field, and no new subspecies of *lauberti* was erected on the strength of this material! The analogy with *crataegi* ssp. *aegopodii* appears to be close, and may serve as a warning against the over-enthusiastic description of new forms where no morphological criteria can be detected.

It should be stressed here that the reserve host phenomenon implies no nutritional inferiority of the reserve to the regular host, and that in some cases the former may be apparently nutritionally the better of the two. For example, both *Sappaphis lauberti* and *S. apiifolia* produce very large adult specimens on *Conium*, in the former case larger on the average than those produced on the normal host, *Heracleum*. Similarly *Smyrnium olusatrum* appears to be in no way inferior to *Petroselinum* and *Aethusa* as a host for *petroselini* and *aethusae* respectively. On the other hand *Torilis japonica*, which is very regularly accepted by *S. aethusae* as a substitute for *Aethusa*, is apparently inferior to it nutritionally, since specimens produced on it are usually smaller in size than members of the same clone reared on *Aethusa cynapium*. There is thus no close correlation between acceptance of a host and its nutritional value to the aphids accepting it. A very wide field lies open for further research on the factors affecting host selection by heteroecious aphids, and, until some of the difficulties involved have been tackled, further theorising, while interesting to the theorist, must remain unprofitable.

Appendix A gives a summary of the associations of species of *Sappaphis* from *Crataegus* with secondary hosts, other than their normal ones, which have been recorded during the course of the present investigations either in the field or in experimental cultures.

(6b) *Morphological Characters.*

(i) *Nymph Colour.*

The colour of the nymphal fundatrigeniae, while not strictly a morphological character, has been used by Börner in his key to the hawthorn *Sappaphis* (1950), and has been treated as being on a par with the strictly morphological characters in the present investigation. Such evidence as has accumulated, however, serves to show that nymph colour is not a reliable criterion. The *crataegi* complex (including *lauberti*, *angelicae* and *petroselini*) exhibits two principal colour forms in the nymphal fundatrigeniae: pink and green. The difference between these two forms apparently consists of the presence or absence of an orange-red pigment in the body contents which is rapidly destroyed on immersion in alcohol or lactic acid and alcohol, leaving the body contents at first uniformly green and later colourless. There is no apparent correlation between this red pigmentation and the degree of red pigmentation of the galls in which the nymphs live, since pure green nymphs are produced from galls which are as deeply pigmented as those containing pink nymphs.

No evidence is available to show whether the presence of the red pigment is genetically unifactorial, or whether a series of alleles exists with different grades of expression. Intermediate forms are of rare occurrence, and the lower grades of red pigment expression may be environmentally produced, or perhaps in some cases be due to the modifying effect of a foreign gene background on the "red" allele following a cross between two taxa. It certainly seems to be the case that the "green" allele is not universally associated with a particular taxon or taxa, since, as has been stated earlier, green nymphs are characteristic of *petroselini* and pink nymphs of *kunzei* in Cambridgeshire, while Börner ascribes green nymphs to *kunzei* in Germany; similarly Börner ascribes pink nymphs to *crataegi* in Germany, while green ones have been collected in Italy by the present author; and *lauberti* is regularly pink in Cambridgeshire, but occasionally green in the neighbouring vice-county of Hertfordshire, according to collections made in 1956. Varying degrees of wax pulverulence superimposed on the body colour of the aphids exert a modifying effect on the apparent nymph colour, giving gradations from strongly pink (very little wax) to lilac grey (much wax) in the case of pink nymphs, or strongly green to greenish-grey in the case of green nymphs. It is clear that a character such as this, which is known to be common to all the species of the complex and to vary in its associations from one geographical region to another, or even within a region, cannot be universally useful taxonomically, although it may be used to assist field recognition in areas where its associations are known from previous observation.

(ii) *Wax Pulverulence.*

Like nymph colour this character is physiological rather than morphological. It has been used by Börner (1950) as a secondary character for adults of *aethusae* and *inculta* (= *petroselini*) on secondary hosts. It is a difficult character to evaluate accurately, and observations made during the present series of experiments show that it should in any case be treated with reserve, since it is easily influenced environmentally. It was found that all the taxa studied varied in the degree of wax powdering from "slight" to "rather heavy" (*lauberti* and *angelicae*) or from "very slight" to "moderate", with a very large range of overlap between taxa. Further, it was found that wax powdering often decreased progressively with time within a single culture or clone, either in colonies maintained on a single plant during its gradual physiological decline, or between colonies of the same clone or culture kept on different hosts. Examples of this which may be quoted are:

Gall series E on *Heracleum* (1951) : wax decreased between the date of sampling of the F.1 generation (19 June) and 9 July, when the plant was beginning to decline.

Gall series G on *Heracleum* (1951) : wax decreased progressively from the nymphs in the galls (before 28 May) to the F.1 and later dates of sampling (19 June, 2, 12 and 25 July).

Gall K.4 on *Heracleum* (1951) : wax decreased between F.1 (19 June) and 25 July.

Gall series I (8 and 10, *lauberti*, 1951) : wax heavier in colonies kept on *Heracleum* than on *Pastinaca*.

Galls AI and AK (*aethusae*, 1953) : wax heavier in colonies on *Aethusa* than on *Torilis*.

Gall AC (*aethusae*, 1953) : wax heavier on *Torilis* than on *Aethusa*.

Gall K.2 on *Pastinaca* (1951) : wax decreased between 19 June and 7 July.

Gall series P (pink nymphs : *crataegi*, 1952) : wax heavier in colonies on *Daucus* than on *Pastinaca*.

These findings suggest that wax powdering is loosely correlated with the suitability and physiological condition of the host plant. It is of interest here to refer to the similar findings of Jacob (1949) on wax markings in *Aphis sambuci* L.

If the physical basis of the wax adornment of *Sappaphis* species is considered it becomes clear that taxonomic value could hardly be anticipated for such a character. The site of production of the wax powder is perhaps the spinal and marginal tubercles of the head and body, which show a generally uniform degree of development and a similar distribution in all the members of the group considered in this paper, apart from statistical differences in the incidence of those on the margins of the seventh abdominal tergite. Sections of the body cuticle reveal no other areas of glandular tissue which could be regarded as able to produce wax in the quantity observed. These marginal and spinal tubercles exhibit a structure similar to that demonstrated by Roberti (1946) for the marginal tubercles of *Aphis frangulae* Kltb., i.e. a compact group of densely staining columnar cells continuous marginally with the rest of the hypodermis, and with their distal ends intimately associated with the overlying cuticle, which stains deep red in Mallory's Triple stain as opposed to the general cuticle which stains bluish. In surface view under high magnification the cuticle over the glandular groups has a finely granulated appearance, which is probably due to a minutely porous structure.

The problem of how the even film of wax over the whole body surface may be produced from such extremely localized glandular groups is an interesting one. The tubercles themselves do not appear to be covered with wax powder, and it has been suggested to the writer in conversation by Dr. J. W. L. Beament of Cambridge that the tubercles may produce a mobile grease compounded of a wax in a volatile solvent, which spreads out in a thin film over the body surface, the solvent gradually evaporating to leave a layer of particles of the less volatile wax. The continued production of grease by the tubercles would account for the absence of a particulate wax layer on their surface. Dr. Beament has pointed out that a certain resemblance in fine structure is to be seen between the tubercles of *Sappaphis* and Géné's organ in ticks, which produces a mobile grease capable of very rapid spread over the surface of the tick's eggs when the organ is applied to them (Lees & Beament, 1948). The mechanism of formation suggested for the wax layer is similar to that postulated by Beament (1955) for the spreading of grease over the cuticle of the cockroach, where however the end point of a particulate wax layer is not reached during the lifetime of the insect. On this basis it would seem likely that the tubercles of *Sappaphis* and other aphid genera represent groups of oenocytes which have become fixed in a constant association with the hypodermis.

Beament (1955) also stresses the part played in the rapid spread of a wax in such a solvent by the degree of saturation of the underlying substrate with water. It is noticeable in aphids that the ventral surface of the body is in very many species

appreciably coated with wax powder even when the dorsal surface is nude or nearly so. It seems a possibility that this is directly related to higher water saturation of the aphid's ventral surface, due partly to greater permeability of the ventral cuticle and partly to transpiration by the host plant. This suggests that the degree of dorsal wax powdering may be affected by the relative humidity in which the aphids live, and that the differences noted between different colonies may be dependent on a complex interaction between the micro-climate and the condition of the host, rather than on differences of a specific kind between the aphids themselves. In any case, enough has been said to show that there are very adequate theoretical grounds for suspecting such a character apart from the observed overlap in the populations studied.

(iii) *Marginal Tubercles.*

The presence of a series of marginal tubercles on the thoracic and abdominal segments is common to at least some generations of all species of *Sappaphis*. These are nearly always distributed on the pronotum and on segments 1 to 5 of the abdomen; their presence on the posterior thoracic segments and segments 6 and 7 of the abdomen is much more irregular. The prevalence or otherwise of marginal tubercles on the seventh abdominal segment has been found to be a useful confirmatory character in dealing with small samples of various species, since certain species have these tubercles present in a majority of specimens, while in others the position is reversed, most specimens being without them. Thus *Sappaphis radicola* (Mordv.) and *S. anthrisci* (Börner) have paired tubercles on abd. 7 in about 95 per cent of specimens examined, while such species as *S. tulipae* (B. de F.) and *S. crithmi* (Buckt.) never, or only exceptionally, have any.

The taxa of the hawthorn *Sappaphis* complex, with the exception of *S. petroselini* (Börner), are characterized by a low incidence of marginal tubercles on abd. 7, most specimens being without them, and very few having a symmetrical pair. The opposite condition prevails in *petroselini*, the majority of which have either paired or asymmetrical unpaired tubercles on abd. 7. This, as has already been made clear in previous paragraphs, is a valuable character for the identification of *petroselini* on *Crataegus*.

During the course of this investigation the percentage incidence of marginal tubercles on abd. 7 was worked out for all the material of the various taxa which had been collected on secondary hosts in the field. It appeared from this that, in addition to the generalized statement that *petroselini* showed high and the other taxa low expression of the character, the taxa with low expression also differed from one another by small amounts. While the individual samples studied were so small that percentages calculated from them were quite unreliable, the total populations were of a size that gave confidence to the frequencies estimated from them.

Preliminary study of the percentage distribution of tubercles on abd. 7 in the populations resulting from experimental transferences suggested that the differences between taxa noted in the wild populations had been overestimated. The percentage occurrence of tubercles on abd. 7 for each of the five taxa with low expression is shown in the accompanying table. The data are drawn from apterae on summer hosts, to avoid as far as possible inaccuracies introduced through recovery of alatae casually settled on the wrong host in the experimental transferences. *Sappaphis ranunculi* (Kltb.), which is not a true member of the complex, is not included here.

Examination of this table shows that the average deviation of the percentage expression in any given taxon from the overall percentage expression for all five taxa calculated as $\Sigma(p_1 \dots p_5)/5$ is greater in the wild population than in the experimental population. This can be more accurately evaluated by calculating values of K from the angular transformations of the individual percentages for the different taxa, using the mean of these transformations instead of the directly calculated mean percentage for the whole population. The ratio $K_{\text{wild}} : K_{\text{experimental}}$ from

TABLE VII.—Incidence of marginal tubercles on abd. 7 in summer apt. viv. ♀♀.

Taxon	Wild collections		Experimental cultures	
	% with tubercles	Number of aphids	% with tubercles	Number of aphids
<i>lauberti</i>	14.24	295	17.82	230
<i>angelicae</i>	1.23	163	14.55	55
<i>aethusae</i>	20.49	122	16.33	392
<i>kunzei</i>	30.13	302	26.63	184
<i>crataegi</i>	10.31	97	8.89	135

this calculation is 5.18, which takes into account the actual numbers of specimens examined in each taxon. The significant variance ratio at $P = 0.05$ for four degrees of freedom either way ($n - 1$ where n , the number of taxa, = 5) is 6.39, while that for $P = 0.10$ is 4.11. By interpolation it appears that the ratio 5.18 is significant at about $P = 0.07$, i.e. that such a disproportion might be expected to occur in samples of this size only once in fourteen replicates if the wild and experimental populations were of identical composition.

If now we proceed to the examination of variance for this character between wild and experimental populations *within* taxa, using the same technique,* but breaking down the overall values for each taxon into those for the individual samples and averaging their angular transformations, we arrive at a result as shown in Table VIII.

TABLE VIII.—Values of K and r for marginal tubercle distribution on abd. 7.

Taxon	Wild		Experimental	
	r	K	r	K
<i>lauberti</i>	21	1775.7	15	2041.4
<i>angelicae</i>	6	663.2	3	127.0
<i>aethusae</i>	11	1921.9	22	4127.1
<i>kunzei</i>	11	2191.1	5	2390.6
<i>crataegi</i>	7	1253.9	10	2637.7
All taxa pooled	56	1715.4	55	2976.1

The values of K_e/K_w given by the results in Table VIII are shown in Table IX.

The variance ratios for 5 per cent and 1 per cent significance where fifty degrees of freedom are present in each population are 1.60 and 1.94 respectively. It therefore appears that the significance of the accumulated variance ratios for the whole

* The formula used for the refined test of significance was

$$K = \frac{\sum n; (a; - \bar{a})^2}{r - 1}$$

where r = number of separate samples examined in the taxon concerned,
 $n;$ = number of specimens in any sample ($;$),
 $a;$ = angular transformation of p ; the percentage presence of tubercles in a sample,
 \bar{a} = the mean of all values of $a;$.

In the second (intra-taxon) analysis these values of K were pooled by means of the formula

$$\bar{K} = \frac{\sum K; (r; - 1)}{\sum (r; - 1)},$$

and the \bar{K}_w/\bar{K}_e ratio was given an appropriate number ($\sum r; - 5$) of degrees of freedom.

TABLE IX.—Significance of variance ratios derived from Table VIII.

Taxon	K_e/K_w	n_1/n_2	Significance of variance ratio
<i>lauberti</i>	1.15	14 : 20	N.S. ($P > 0.2$)
<i>angelicae</i>	1/5.22	2 : 5	N.S. ($P > 0.1$)
<i>aethusae</i>	2.15	21 : 10	N.S. ($P > 0.1$)
<i>kunzei</i>	1.09	4 : 10	N.S. ($P > 0.2$)
<i>crataegi</i>	2.10	9 : 6	N.S. ($P > 0.1$)
All taxa pooled	1.73	50 : 51	Significant ($P < 0.05$)

population of wild and experimental material is somewhat greater than $P = .05$ but somewhat less than $P = .01$.

It should be noted that the hypotheses tested by these variance ratios are not the same. Thus the first comparison of K values showed that the observed percentages of tubercle incidence per taxon varied more widely about the overall percentage for the complex in the wild populations than in the experimental ones, the difference being not quite enough to reach the conventional 5 per cent limit of significance ; while the second comparison of K values demonstrates a significant excess of variance *within* taxa for the experimental populations over the wild ones. It should further be noted that the wild population examined was drawn from a much wider range of localities than the experimental population, which all originated from a small area in Cambridgeshire ; this suggests that the significance of the intra-taxon differences is in no way overestimated, since expectation would normally be that variance would be greater in a population from widely separated localities than in one from a small area.

When these results are related to the known conditions of the experimental programme the argument may be developed as follows :

The experimental populations, which show the greater variance within taxa, are derived from random collections of galls made from *Crataegus* in the field before the time of the spring migration. The wild populations were collected in the field from secondary hosts, that is, after migration had occurred. Under these circumstances it is possible to envisage two ways in which the greater variance of the experimental cultures could originate :

(A) Environmental or seasonal effects may lead to an alteration of percentage expression of marginal tubercles on abd. 7, leading either to an increased variance in experimental or a decreased variance in wild populations.

(B) Selection pressure may eliminate some of the more widely aberrant clones from the wild population, thus apparently decreasing the variance.

In the case of alternative (A) the effect would be purely phenotypic, since the population consists of an assemblage of clonal lines with genotypes determined the previous autumn (mutation excepted). It is not possible to test this alternative effectively for wild populations whose previous history is unknown. But in the case of experimental lines which are known to be clonal (i.e. derived from a single gall containing one fundatrix) it is possible to examine the distribution of marginal tubercles on abd. 7 in successive samples taken over a period of time, and find whether there is any evidence of significant departures from expectation attributable to seasonal or environmental influences. This has been done in a number of cases, the details of which are shown in Table X. The values of chi-square derived from $2 \times n$ contingency tables constructed from the samples used are shown in all cases where such a test is necessary or possible in view of the available number of observations.

In only one instance (AL) is a significant chi-square obtained, and here the significance rests on a single specimen, the only one out of 41 examined which possessed

a tubercle on abd. 7. There is thus no convincing evidence that seasonal or environmental influences appreciably affect the distribution of marginal tubercles within a clonal line under experimental conditions. A similar apparent constancy of clonal lines will also be demonstrated in a later paragraph for antennal hair lengths. In view of it we may with some confidence regard the operative factor in reducing the variance of wild populations on secondary hosts as being selection pressure, exerted through the rigours of host-finding at the time of the spring migration, this being the only major factor from which it is possible to anticipate an effect of the magnitude observed.

A second effect which can best be explained in terms of the selection pressure operating on the complex at the time of the spring migration is the greater variance of the percentage incidence of tubercles for the different taxa about the overall mean in the wild populations compared with the experimental populations. Here we

TABLE X.—Chi-square tests for significant changes of marginal tubercle distribution on abd. 7 in clonal lines.

Taxon	Clone	Migrants	F.1 apt.	Midsummer		Chi-square/ <i>n</i> d.f.
				apt.	al.	
<i>lauberti</i>	K.3	7 : 36	5 : 23	1 : 12	—	0.74/2
"	G.8	2 : 2	2 : 1	12 : 39	1 : 4	4.10/3
<i>aethusae</i>	AB	4 : 14	4 : 42	—	0 : 1	2.65/2
"	AC	1 : 1	15 : 15	—	0 : 1	Not calculated
"	AF	0 : 13	0 : 33	—	—	0
"	AH	2 : 6	10 : 43	—	—	0.17/1
"	AI	0 : 2	3 : 28	—	0 : 4	Not calculated
"	AK	0 : 1	3 : 30	—	—	
"	AL	0 : 1	0 : 36	—	1 : 3	9.64/2 ($P < 0.01$)
<i>kunzei</i>	K.2	4 : 21	11 : 37	2 : 7	3 : 20	1.21/3
"	EA	1 : 8	1 : 11	3 : 6	1 : 15 (3rd apt. sample)	4.18/3
<i>crataegi</i>	AA	0 : 9	0 : 39	—	—	0

(In all distributions shown the first figure is the number of individuals with one or two tubercles on abd. 7, the second that of individuals with none.)

are on less certain ground, since the significance of the $K_m : K_e$ ratio obtained in this case is slightly less than the customarily accepted 5 per cent significance level. However, such levels of acceptance of significance are arbitrary, and it is therefore not unreasonable to examine the consequences of accepting a less rigorous definition of significance, while making the necessary reservations in so doing.

Taken in conjunction with the greater variance within taxa recorded for the experimental material, the wider percentage differences between taxa in the wild material indicates that selection does not operate equally at both ends of the range of variation in a given taxon.* Broadly speaking, in the experimental population there is a relatively less rigorous elimination of clones which tend towards the mean percentage for the complex as a whole than occurs in the wild population. Now it is clear that selection of measurable intensity must be operating against characteristics of negative adaptive value, and that the mere presence or absence of a pair of tubercles on one segment of the abdomen of an aphid is very unlikely to constitute such a characteristic. However, a morphological character such as this can be used as a

* N.B.—The limits of a taxon as determined in the present investigation and as used in this argument are an approximation to its natural limits, and must be so understood.

clue to what is happening in the case of other non-morphological characters of greater adaptive significance. If the spring migration in nature is eliminating an excessive number of clones tending toward the overall mean for the complex, it must be assumed that these clones show a proportional deficiency either of general viability or of such pertinent qualities as ability to find, or having found to colonize, a suitable secondary host.

On the basis of this premise, two possible hypotheses can be erected to explain the apparent inward shift of the taxon means in the experimental population :

(1) In a balanced population (i.e. one whose mean remains constant from generation to generation) total effects of selection pressure, both exogenous (environmental) and endogenous (genetic) together, must be similarly balanced about the population mean ; and if the distribution of the population is normal the balance of selection pressures must also be symmetrical. This postulate may be taken as applying at least as a close approximation to the population of *Sappaphis* species on *Crataegus*. Now in such a situation any asymmetry or unbalance in the selection pressure acting on the population leads to a more or less rapid adjustment of the mean until symmetry is established again.

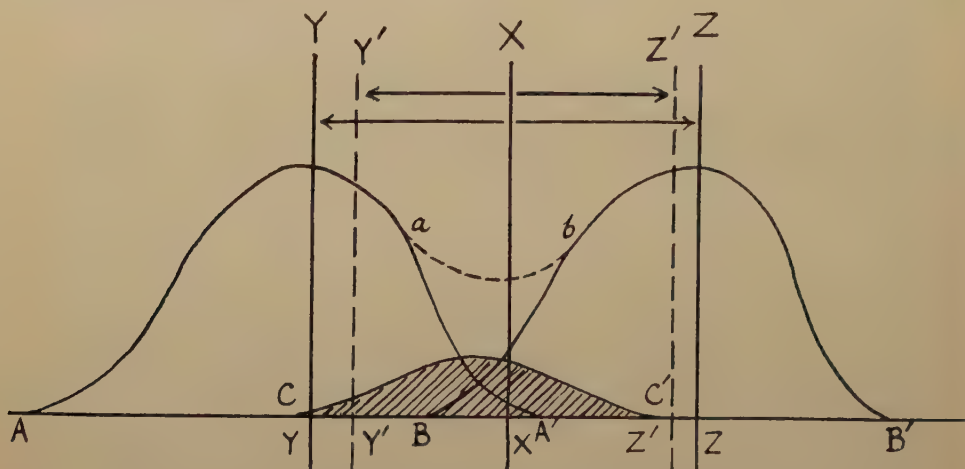


FIG. 2 —Diagrammatic representation of the effect of hybridity in a species-complex.

If total selection pressure on the two halves of a normal frequency distribution is made up of more than one component, the relative effectiveness of which differs at the two ends of the variation range, then relaxation of the stringency of one component while the others remain constant will lead to an unbalance resulting in a shift of the population mean. So if selection against inefficient host-finding in nature is more severe in any given taxon at the end of the distribution lying nearest to the overall mean for the complex, this will be balanced at the other end of the distribution by heavier selection against some other aspect or aspects of viability. Then relaxation of selection against inefficient host-finding (as in the present series of experimental host transferences) will, unless exactly balanced by relaxation of the antagonistic selection pressures, lead to an inward movement of the taxon mean towards the overall mean for the whole complex, similar to that observed. It remains to suggest a justification for the assumption of greater selection pressure against poor host-finding ability at the end of the distribution nearest the overall mean. This will be attempted later.

(2) If the various components of the total selection pressure are all symmetrically distributed about the taxon means (a most unlikely circumstance), or if the effects

of selection against inefficient host-finding are so balanced (rather less improbable), it becomes necessary to find some way in which relaxation of such symmetrically distributed pressure can have an asymmetrical effect. A hypothesis which fairly simply fulfils this requirement is illustrated in the accompanying diagram (Fig. 2).

In the diagram the curves AA', BB' represent the normal distributions of two taxa (A) and (B) for a given character. The curve CC' represents the distribution of the same character among naturally occurring hybrids between the two taxa (it may be noted here that the flattened normal type of curve used here for CC' is not in any way essential to the argument, and that CC' could without invalidating the theory assume any form, so long as its mode or modes lie within the modal axes of AA' and BB'). The dotted line *ab* represents the middle section of the combined bimodal distribution curve for the whole populations including the hybrids. The axes X, Y and Z represent respectively the mean of the whole distribution and the means of the two pure taxa (A) and (B). Now if the shaded curve CC', which lies almost entirely within the tails of the two curves AA' and BB', is not detected as having a separate existence (as is highly probable if the percentage of hybrids is small) it will be included in the two main distributions and will lead to an apparent inward shift of the axes Y and Z to positions Y' and Z'. Next, if increased selection pressure, acting symmetrically on the pure taxa (A) and (B), also eliminates a large majority of the hybrid clones (which will probably be less well adapted to efficient finding of a specific secondary host), the new apparent positions of the axes Y' and Z' will shift outward to an extent determined by the percentage elimination of the hybrid clones—i.e. at 100 per cent elimination Y' and Z' will coincide with Y and Z. This sort of situation can be stable, since the true means Y and Z are not affected by the fate of the hybrid population unless back-crossing from the hybrids into taxa (A) and (B) is appreciable—a prerequisite of which is the survival of hybrid clones through the summer and the production by them of fertile males and gynoparae in the autumn. The diagram makes it clear that the distances XY' and XZ' (i.e. the deviation of the apparent means of the separate taxa from the overall mean of the whole distribution) will be greater in the event of increased selection pressure, so long as selection effects are symmetrically distributed over the pure taxa (A) and (B) and the hybrids are at some selective disadvantage. Such a selective disadvantage may certainly be assumed, if only for the reason that any advantage possessed by cross-bred progeny would have prevented the initial divergence of the taxa (A) and (B) in the absence of any geographical or ecological isolation, such as is certainly absent in the complex under discussion.

The situation pictured in diagrammatic form here can be extended to cover a complex of more than two taxa, although the difficulties of representing it in graphic form become greater. The principle, however, remains simple and requires no expansion.

If we return to hypothesis (1) it can be seen that the postulation of a proportion of hybrids among the spring population before migration does not conflict in any way with that interpretation of the data; in fact, if true, it offers a justification of the assumption made, that selection through the spring migration, that is against poor host-finding ability, is greater at the end of the distribution nearer to the overall mean. This is because the hybrids, whose morphological characters will tend to lie between those of the parents, may also be expected to show some confusion of their secondary host preference mechanism; and even a small derangement of this mechanism would place them at a very serious disadvantage in nature, where elimination even of well-adapted pure-blooded *alatae* by the hazards of the spring migration is very high.

It is essential to stress that the foregoing arguments are offered as hypotheses which fit the observed facts of marginal tubercle incidence on the seventh abdominal segment in these aphids. It is not to be supposed that selection pressure is a simple phenomenon which can be readily broken down into two or three independent factors,

or indeed that selection against host-selecting capacity is the only component likely to be affected by the conditions of experimentation prevailing in the work described here. On the other hand there is no other selective pressure which can be confidently asserted to be so drastically reduced by experimental conditions in which every alate introduced into a choice cage has repeated chances of choosing and colonizing a suitable host plant; nor any whose reduction could so simply be postulated as leading to the observed significant change in variance in the alienicolae. Final proof of hybridity in the hawthorn *Sappaphis* community requires much further research; but it is a hypothesis which may very reasonably be advanced in the case of any complex of forms whose evolution into distinct species is not fully demonstrable morphologically, and whose isolation from one another is spatially incomplete or non-existent.

If the significance of the inward shift of means in experimental populations is not held to be of a significance needing special explanation it may perhaps be argued that no other explanation is necessary for the significantly greater variance among experimental samples than is provided by the normal Mendelian dynamics of a single species. In such an explanation the life of the individual sexually reproducing organism is represented here by that of a whole clone from winter egg to sexuales; and the tails of the normal distribution will consist to a considerable extent of homozygous recessives whose removal by selection in nature will to some extent be mitigated under experimental conditions. However, this explanation offers no solution to such observations as the marked bimodality found in the distribution of samples showing characters typical of *petroselini*; so while there is little doubt that the survival of poorly adapted homozygous recessives will contribute some part of the excess variance seen in experimental material, it is hard to believe that this is responsible for the whole of the effects observed. In fact the greater significance of the increase in variance when compared with the change in apparent mean values is perhaps due to the fact that the former is affected by the fate of both pure-blooded recessives and hybrids, while the net effect on the apparent mean value is due to elimination of hybrids in nature, the pure-blooded recessives being probably symmetrically distributed and therefore neutral in total effect.

(iv) *Hair Lengths.*

The lengths of the antennal and dorsal body hairs are the most important single criterion in separating the hawthorn group of *Sappaphis* into sub-units. As such they have been extensively used in the preliminary sorting of spring migrants, as will be seen from earlier sections of this account. It is therefore particularly desirable to subject the data to some kind of critical examination. Hair length in the genus *Aphis* L. is known to be a character on which it is unwise to rely (Jacob, 1949) although it has been used in past attempts to unravel the black *Aphis* complex; and for this reason an attempt has been made to test the constancy and range of variability of hair lengths in the hawthorn *Sappaphis*.

Leaving out of account the very distinct species *S. ranunculi* (Kltb.), the taxa of the hawthorn complex fall into two easily separated groups: those with long antennal and dorsal body hairs (*lauberti* and *angelicae*) and those with short ones (*crataegi* subgroup and *petroselini*). There is a very slight band of overlap in a few cases, with hair lengths around 20 μ , but samples with this order of hair length are rare, and for practical purposes the dividing line may be drawn at 20 μ . There is a size effect which needs to be taken into account in analysing variation in hair length, but this does not appreciably vitiate the use of the character.

It has been shown in the preceding section of the discussion that there is no convincing evidence of any significant change in the distribution of marginal tubercles on the seventh abdominal segment within clones of this complex during the course of the generations on Umbelliferae up to midsummer. The same question is a necessary starting point of any useful survey of hair length variation.

Accordingly a number of clonal lines from experimental cultures after transference have been examined for variation in the maximal length of the hairs on the third antennal joint. Alatae and apterae were compared separately, since the hairs of the former are normally appreciably shorter than those of the latter, and the two forms are therefore not directly comparable.

Jacob (1949) used the relation of the longest hair on the third antennal joint to the diameter of the basal constriction of the joint in measuring the antennal hairs of *Aphis sambuci* L. This was in order to render the data as nearly as possible independent of absolute size of the aphids. In the present series of measurements the diameter of the actual articulation of the joint was used as a comparative measurement, and the ratio of the length of the longest measurable hair to this diameter used as the parameter for examination.

The accompanying table (Table XI) shows the results obtained from the measurement of this ratio in four separate clones, two long-haired and two short-haired. Differences between the mean values for successive samples of both apterae and alatae were subjected to a *t*-test of significance, and possible differences in variance were tested from variance ratio tables (Fisher & Yates, 1949, pp. 35-41).

TABLE XI.—Tests for significant within-clone variability in experimental material.

Sample	<i>n</i>	Mean	σ	$t(\bar{x}_1 - \bar{x}_2)$	Variance ratio ($n_1 - 1/n_2 - 1$ d.f.)	<i>P</i> value of v.r.
K.2 apt. (1) K.2 apt. (2)	47 8	0.84 0.87	0.10 0.07	0.8 (<i>P</i> = c. 0.4)	2.0 (46/7)	c. 0.2
K.2 al. (migr.) K.2 al. (alien.)	21 22	0.54 0.54	0.06 0.08	0 (<i>P</i> > 0.9)	1.8 (21/20)	>0.1
K.3 apt. (1) K.3 apt. (2)	28 13	1.87 1.80	0.18 0.16	1.2 (<i>P</i> > 0.2)	1.3 (27/12)	>0.2
EA apt. (1) EA apt. (2) EA apt. (3) (1) (see above)	12 9 16 12	0.72 0.66 0.73 0.72	0.10 0.09 0.10 0.10	1.5 (<i>P</i> > 0.1) 1.75 (<i>P</i> = c. 0.1) 0.25 (<i>P</i> = c. 0.8)	1.2 (11/8) 1.2 (15/8) 1.0 (11/15)	>0.2 >0.2 >0.2
G.8 apt. (1) G.8 apt. (2)	3 51	1.32 1.27	0.13 0.18	0.45 (<i>P</i> > 0.6)	1.9 (50/2)	>0.2
G.8 al. (migr.) G.8 al. (alien.)	4 5	0.79 0.75	0.09 0.11	0.6 (<i>P</i> > 0.5)	1.5 (4/3)	>0.2

It is clear from the values of *P* shown in the table that no evidence was obtained supporting the existence of significant changes either in means or variances between successive samples of these clones over the periods involved (the intervals between sampling were not less than 14 days, and the whole period covered in each case was from the beginning of June to about the third week in July for apterae, and that elapsing between the spring migrant and midsummer generations for alatae). This result compares well with that obtained in the similar examination of marginal tubercle distributions.

Following this preliminary test attempts have been made to answer two questions : first, whether the results obtained for marginal tubercle distributions in wild and experimental populations can be confirmed in a character involving hair lengths ;

and secondly, what approximate range of variation may be expected in hair length within single homogeneous samples of *Sappaphis*.

The first question has been investigated by using random samples of uniform size taken from two taxa: *S. lauberti* representing the long-haired group, and *S. aethusae* representing the short-haired group. In each of these taxa the samples of wild and experimental aphids containing more than ten apterae were assembled, and a random elimination made from the larger group in each case, in order to make the number for each group the same. In this way an assemblage of six large samples from both wild and experimental *lauberti*, and five from both wild and experimental *aethusae* was obtained. Random samples of ten specimens from each large sample were then drawn, and the value of the ratio (longest measurable hair on ant. III : articular diameter of III) was calculated for each specimen.

TABLE XII.

lauberti (wild population)

Sample numbers:							
720	721	520	521	1402	1646		
1.78	1.29	1.82	1.96	1.86	1.29		
1.71	1.67	2.00	1.60	1.79	1.52		
1.42	1.50	2.04	2.24	1.50	1.30		
1.57	1.18	1.67	2.00	1.43	1.33		
1.50	1.39	1.67	1.76	1.85	1.43		
1.79	1.52	1.93	2.08	1.85	1.43		
1.63	1.32	2.00	2.33	1.69	1.61		
1.87	1.43	2.00	2.17	1.67	1.33		
1.79	1.54	1.93	1.93	2.00	1.38		
1.86	1.43	1.96	1.69	1.86	1.66		
						101.75	SX
16.92	14.27	19.02	19.76	17.50	14.28	1.70	\bar{x}
1.69	1.43	1.90	1.98	1.75	1.43	176.74	SX^2
28.85	20.54	36.34	39.56	30.91	20.54	172.55	$(SX)^2/k$
28.63	20.36	36.18	39.04	30.63	20.39		
0.22	0.18	0.16	0.52	0.28	0.15	4.19	Sx^2
Total = 1.51							

lauberti (experimental population)

Sample numbers:							
E	F	G	I	K.3	K.4		
1.69	1.68	1.04	1.82	1.52	1.33		
2.04	2.00	1.28	1.85	1.57	1.33		
1.92	1.71	0.80	1.93	1.54	1.33		
1.83	1.75	0.95	2.04	1.63	1.38		
1.78	2.04	0.90	1.88	1.60	1.20		
1.75	1.76	1.08	2.00	1.52	1.20		
1.76	2.00	1.33	2.00	1.54	1.50		
1.73	2.08	1.09	1.92	1.60	0.80		
1.44	1.44	1.17	1.85	1.61	1.29		
1.67	1.69	1.45	2.29	1.47	1.20		
						94.59	SX
17.61	18.15	11.09	19.58	15.60	12.56	1.58	\bar{x}
1.76	1.82	1.11	1.96	1.56	1.26	156.16	SX^2
31.24	33.33	12.67	38.47	24.36	16.09	149.12	$(SX)^2/k$
31.01	32.94	12.31	38.34	24.34	15.78		
0.23	0.39	0.36	0.13	0.02	0.31	7.04	Sx^2
Total = 1.44							

The resulting data were subjected to an analysis of variance, and the three estimates of variance derived from this (total, within-sample and between-sample) were related within each taxon to give variance ratios which were examined for significance from the table of e^{2z} ratios (Fisher & Yates, 1949, p. 39). The resulting analyses and variance ratios derived from them are shown in Tables XII–XIV.

TABLE XIII.

aethusae (wild population)

Sample numbers:						
613	632	736	922	1635		
0.63	0.63	0.60	0.64	0.68		
0.60	0.52	0.67	0.54	0.62		
0.55	0.54	0.64	0.55	0.64		
0.80	0.65	0.64	0.55	0.63		
0.63	0.64	0.56	0.67	0.76		
0.67	0.60	0.62	0.64	0.68		
0.54	0.57	0.50	0.60	0.75		
0.63	0.52	0.62	0.54	0.57		
0.50	0.54	0.80	0.65	0.75		
0.76	0.56	0.62	0.67	0.62		
6.31	5.77	6.27	6.05	6.70	31.10	SX
0.63	0.58	0.63	0.61	0.67	0.62	\bar{x}
4.0613	3.3515	3.9849	3.6877	4.5276	19.6130	SX^2
3.9816	3.3293	3.9313	3.6603	4.4890	19.3442	$(SX)^2/k$
0.0797	0.0222	0.0536	0.0274	0.0386	0.2688	Sx^2
Total = 0.2215						

aethusae (experimental population)

Sample numbers:						
AC	AH	AI	AK	AF		
0.76	0.68	0.64	0.77	0.55		
0.71	0.73	0.71	0.78	0.52		
0.71	0.80	0.62	0.83	0.52		
0.68	0.81	0.67	0.77	0.58		
0.67	0.59	0.73	0.87	0.59		
0.67	0.57	0.67	1.00	0.52		
0.76	0.65	0.80	0.81	0.54		
0.86	0.62	0.75	0.90	0.52		
0.71	0.84	0.61	0.74	0.52		
0.76	0.63	0.80	0.83	0.65		
7.29	6.92	7.00	8.30	5.51	35.02	SX
0.73	0.69	0.70	0.83	0.55	0.70	\bar{x}
5.3449	4.8738	4.9434	6.9426	3.0531	25.1578	SX^2
5.3144	4.7866	4.9000	6.8890	3.0360	24.5280	$(SX)^2/K$
0.0305	0.0872	0.0434	0.0536	0.0171	0.6298	Sx^2
Total = 0.2318						

It will be readily seen that the variance ratios of the pooled within-sample variances for wild and experimental samples are without any significance, i.e. the general level of variance within single samples is not affected by the transition from wild to experimental conditions. The situation in the case of between-sample variance is rather markedly different. In both taxa examined the variance ratio for experimental material over wild material is far from unity; that for *aethusae* is clearly very significant, with a P value of approximately 0.03. The ratio for *lauberti* taken by itself is not significant; but it is possible to obtain a value for the combined probability

of this result occurring simultaneously with a result of the degree of significance found for *aethusae*, using the formula $-2 \sum (\log_e P)$; where the number of results is n this term is distributed as chi-square with $2n$ degrees of freedom. Applying this test to the results given above a value for chi-square of 9.79 is obtained, with four degrees of freedom. The probability of this value is just less than 0.05. The level

TABLE XIV.—Variance ratios derived from analyses of variance given in Tables XII–XIII.

	Variance ratio (e/w)	Degrees of freedom (n_1/n_2)	Significance (P value)
<i>lauberti</i>			
Within sample	0.95	54/54	N.S.
Between sample	2.09	5/5	0.25 (approx.)
<i>aethusae</i>			
Within sample	1.05	45/45	N.S.
Between sample	9.18	4/4	0.03 (approx.)

of significance of this result is closely similar to that found in the analysis of the marginal tubercle data. This is the more interesting since the experimental material used in the present analyses was in both cases drawn from gall collections made during a single season in Cambridgeshire, and that of *aethusae* was in fact derived from five galls obtained from a single fifteen-yard length of hedge in 1953. It can therefore hardly be supposed that the excess variability of the experimental cultures has been overestimated through any sampling bias, since this should produce a tendency to greater variance in the wild population even more marked than that already postulated in the discussion of the marginal tubercle data. Nor can the possibility of the excess variance being due to misidentifications of experimental clones be given any credence, since reference to the 1953 experimental results shows that the biological and morphological evidence from these clones was extremely consistent and unambiguous.

The effect of this is to confirm strongly the objective reality of the greater variance detected in the experimental aphids for marginal tubercle distribution. The present analysis is not an independent check, since the specimens used form part of the material used for the previous analysis; but the indication is that the variance effect between samples is a real characteristic of the material, and not merely an idiosyncrasy demonstrable in a single character.

The other feature detected in the marginal tubercle data—the convergence of the estimates of the population means in the experimental material—also occurs in the hair length data for *lauberti* and *aethusae*, but to an extent having no statistical significance. It must be remembered however that only two taxa are involved in the hair length analysis, and it is possible that if all five had been included as in the marginal tubercle analysis a lower degree of probability would have been indicated. It is unfortunate that a lack of sufficient large samples among the experimental material of other taxa prevented such an extension of the analysis.

A point of some importance arising from the analyses of variance in Tables XII–XIII is that, although the pooled variances within samples show no departure from random distribution the ratio between individual sample variances is sometimes highly significant. Thus the maximal variance ratios between single samples in the various groups are :

<i>lauberti</i> (wild)	3.47 (9/9 d.f.), $P < 0.05$
„ (experimental)	19.50 („ „), $P < 0.01$
<i>aethusae</i> (wild)	3.59 („ „), $P < 0.05$
„ (experimental)	5.10 („ „), $P < 0.05$.

It may be suspected that this is due to some samples being of clonal and some of mixed origin ; for example, the highly significant ratio recorded for experimental *lauberti* is apparently due to the very small variance (0.02) of sample K.3, which is known to be clonal. But this cannot apply to the experimental material of *aethusae*, all of which is clonal. However, in the case of these samples four out of five are drawn from cultures where parallel lines were reared on *Aethusa* and *Torilis*, and it is observed that the maximal variance ratio, 5.10, occurs between a sample (AH) containing five apterae from each host and one drawn entirely from one host, *Aethusa* (AF).

Two tests were made to determine whether the significance of the variance ratios between single samples could be put down to this host plant factor.

(1) The first five specimens alone (all from *Aethusa*) of each experimental sample of *aethusae* were taken, and their sums of squares calculated. The results were :

Sample	AC	AF	AH	AI	AK
Sx^2 (all $\times 10^{-4}$)	50	43	331	86	80

The maximal variance ratio still lies between AH and AF (7.70 with 4/4 d.f.) and remains significant at $P < 0.05$. The ratio between AH and AC has also attained significance (6.60 with 4/4 d.f., $P < 0.05$).

(2) Each of the mixed samples AC, AH, AI and AK was divided into specimens from *Aethusa* and specimens from *Torilis*, and the means and variance ratios between the subsamples of each sample were calculated. At the same time the pure sample AF from *Aethusa* was divided at random into two subsamples of five specimens each and the same calculations made for these. The results were :

Sample	AC	AH	AI	AK	AF
v.r. between subsamples	4.06	1.30	4.11	1.05	2.98
d.f.	4/4	4/4	3/5	6/2	4/4
P	>0.1	>0.2	>0.1	>0.2	>0.1
Subsample means: (1)	0.71	0.72	0.67	0.83	0.55
(2)	0.75	0.66	0.74	0.82	0.55

From these data it appears that, although the variances between subsamples do not give significant ratios, the differences between subsample means from different hosts are often enough to increase the variances of the whole samples to values significantly greater than those of homogeneous samples. On the other hand, even between homogeneous clonal samples there is sufficient residual variability not attributable to host plant effects to give occasional results with, or approaching, 5 per cent significance. In other words, it appears that variability in the maximal antennal hair length is itself subject to marked variability.

Before leaving this section one point remains to be discussed. This is the possibility that the mixed host samples from the experimental population of *aethusae* might be in part responsible for the high variance ratio between wild and experimental aphids when between-sample variance is estimated. A brief consideration of this leads to the conclusion that any such effect would in fact tend to reduce the apparent

significance of the variance ratio. The wild material of *aethusae* was made up of three pure samples from *Aethusa* and two from *Torilis*; the experimental material was nearly similar in composition (33 specimens from *Aethusa*, 17 from *Torilis*), but distributed in four mixed samples and one pure one. Now if two populations like this are analysed for between-sample variance (which depends on the distribution of sample means), and if there is in fact a host-plant effect on the individual hair length values, it is clear that an array of pure samples from different hosts will tend to have a wider dispersion of means (and therefore a greater between-sample variance) than an array of samples which are themselves a mixture of specimens from different hosts. Therefore in so far as the foregoing analysis of *aethusae* is concerned any host plant effect may be safely disregarded, since it would in any case lead to an underestimate rather than an overestimate of the e/w variance ratio.

The second question arising from the consideration of hair length data is what approximate limits may be set to variability in hair length within single homogeneous samples of *Sappaphis*. The term "homogeneous sample" is here taken to mean a sample which cannot readily be subdivided into more than one group of individuals by means of frequency distributions for one or more characters. It does not imply that the sample is necessarily clonal (though it may well be so) but only that conventional taxonomic procedures will not disclose the presence of more than one taxon in the material.

The character whose variability was estimated in this case was the greatest measurable length of any spinal or pleural hair on the second and third abdominal tergites. This length was used as a simple parameter, and not combined into a ratio as was done with the antennal hair maxima. The range of the hair length maxima, mean, variance and standard deviation were calculated for each sample of the available material. It was found that, as might have been foreseen, the variance within samples of long-haired taxa was much greater than that within samples of short-haired taxa. To overcome this and render the data comparable the Coefficient of Variability (i.e. the standard deviation expressed as a percentage of the mean) was taken instead of the variance, and it was then found that the characteristics of all the taxa were rather consistent.

In trying to estimate limits of variability for taxonomic purposes it is obviously preferable to overestimate rather than to underestimate. For this reason *nil* values for variability, which were sometimes recorded in small samples, were ignored, being clearly artificial and due either to sample size, insensitivity of measuring technique or a combination of both these factors.

Table XV summarizes the data obtained for material from each of the taxa of the *crataegi* group, using samples from all available sources, i.e. field collections and both clonal and non-clonal experimental cultures. For comparison with these data an estimate was made of the total range of C.V. values for single-gall, i.e. clonal, samples of spring migrants of four different taxa. This was done for each taxon by calculating the mean C.V. per sample and its standard deviation, and estimating the total range as $\bar{x} \pm 3\sigma$. The results are shown in Table XVI, and from these it will be seen that the upper limits of C.V. values estimated by this method agree rather closely with the highest observed values for material from all sources. Also given in Table XVI is the range $\bar{x} \pm 2\sigma$, which theoretically includes about 96 per cent of sample values of C.V.; this again is approximately valid when extended to material from all sources: thus out of sixty samples of *alatae* of all four taxa concerned only four, or 6.67 per cent, lie outside the $\bar{x} \pm 2\sigma$ limit calculated from the clonal samples. Further, the range of C.V. values found in single clonal samples confirms the finding of the variance studies on antennal hair length, i.e. that variability is itself a variate with a considerable range of values independent of the homogeneity of the sample. It is interesting to compare this conclusion with the findings of Cottier (1953), who analysed morphological differences in batches of material of several species of aphids in New Zealand and found "highly significant" or even

TABLE XV.—Summary of variability data for longest hairs on 2nd/3rd abdominal segments.

Taxon	Morph.	Wild or experi- mental	Number of specimens	Number of samples	Range of variation of					Mean C.V.
					Hair maxima (μ)	Sample means (μ)	Sample variances	Sample S.D.'s	Sample C.V.'s	
<i>lauberti</i>	Apt.	W	141	8	23-65	28-55	8-22-80-00	2-9-8-9	8-6-16-5	11-9
	Al.	E	92	12	22-66	25-59	1-00-84-56	1-0-9-2	3-6-22-4	9-9
		W	153	13	22-61	31-46	4-00-79-75	2-0-8-9	5-3-21-7	11-9
		E	97	11	19-57	22-48	3-00-39-00	1-7-6-2	3-9-20-0	11-2
<i>angelicae</i>	Apt.	W	133	5	26-65	31-42	19-00-47-94	4-4-6-9	10-5-16-4	13-5
	Al.	E	30	3	41-61	47-51	9-77-30-55	3-0-5-5	5-9-11-7	9-5
		W	81	4	20-36	28-30	8-00-10-71	2-8-3-3	9-7-11-8	10-5
		E	37	4	25-50	33-46	25-00-34-00	5-0-5-9	11-3-16-9	14-2
<i>aethusae</i>	Apt.	W	85	7	7-18	9-14	1-27-7-00	1-1-2-6	8-5-23-3	16-0
	Al.	E	63	13	8-20	11-15	0-75-13-75	0-9-3-7	7-5-28-2	16-7
		W	30	3	11-18	13-14	1-54-4-08	1-2-2-0	8-6-15-4	13-1
		E	88	13	11-18	13-18	0-25-4-17	0-5-2-0	3-5-14-3	8-8
<i>kunzei</i>	Apt.	W	56	6	5-16	8-11	1-33-6-50	1-2-2-6	13-3-23-6	17-8
	Al.	E	8	2	10-14	12-13	1-00-3-00	1-0-1-7	7-7-14-2	11-0
		W	15	2	7-16	11-12	3-64-10-50	1-9-3-2	17-3-26-7	22-0
		E	30	2	9-14	12-13	1-63-1-75	1-3±	10-0-10-8	10-4
<i>crataegi</i>	Apt.	W+E	94	12	8-14	10-12	0-50-5-50	0-7-2-3	6-4-20-9	14-0
	Al.	W+E	51	10	7-18	9-16	0-40-5-75	0-7-2-4	5-4-17-1	12-2
<i>petroselinii</i>	Apt.	W+E	92	11	7-13	8-10	0-33-5-50	0-6-2-3	6-7-23-0	15-8
	Al.	W+E	39	10	7-14	8-13	0-50-5-00	0-7-2-2	6-4-22-0	10-9

“ very highly significant ” differences in several instances within single species. We must clearly be careful to avoid a mental confusion between statistical and taxonomic concepts of significance ; it is unfortunate that the term “ population ” should be common to statistics, ecology and taxonomy, since the referent varies according to context, and this may lead to confusion in thought and discussion.

The data for the abdominal body hairs show that the extreme limit of variability consistent with homogeneity of the sample concerned may be represented by a C.V. value of about 24. Any samples with higher C.V. values are almost certainly not homogeneous. The rarity of values higher than 24 even in field collections, when taken with the rather considerable ranges of variation in hair length found in the material as a whole, suggests that the majority of samples collected in the field are clonal in origin. This is not hard to believe in the case of heteroecious aphids such as these, where each summer colony probably owes its existence to a single migrant. It would be of interest to examine the variability of one or more monoecious species in this way, since they might be expected to show wider divergences between estimates from clonal lines and observations from field collections, correlated with the greater probability that any given colony is descended from more than one fundatrix.

TABLE XVI.—Statistics and range limits of C.V. for abdominal hair length in clonal spring migrants.

Taxon	C.V. range	Mean	Variance	S.D. (σ)	Limits of variability	
					$\bar{x} \pm 2\sigma$	$\bar{x} \pm 3\sigma$
<i>lauberti</i> (10 samples)	3·9–17·6	10·3	16·54	4·1	18·5 2·1	22·6 —
<i>aethusae</i> (13 samples)	3·5–14·3	8·8	12·94	3·6	16·0 1·6	19·6 —
<i>crataegi</i> (7 samples)	5·4–17·1	11·9	15·97	4·0	18·9 3·9	23·9 —
<i>petroselini</i> (5 samples)	6·4–14·5	9·1	11·30	3·4	15·9 2·3	19·3 —

12. CONCLUSIONS.

It is now possible to arrive at some kind of synthesis from the various data recorded and analysed in the foregoing pages. The experiments described have confirmed the existence of seven different taxa of *Sappaphis* causing galls on *Crataegus* in Britain, the biological and morphological distinctness of which are not uniform.

Morphological studies of certain characters in field populations and experimental cultures have shown that these taxa are more readily separated morphologically when material from secondary hosts is examined than when spring gall material is used. There is a greater degree of intergrading between them in the spring generations than can be seen among wild collections from secondary hosts. It has also been shown that the alienicolae reared in culture after transferences in the insectary have significantly greater intra-taxon variance between samples than wild alienicolae, and that the taxon means show a simultaneous convergence which, while not statistically significant over the number of experiments performed, has been demonstrated in two separate variables. The hypothesis has been advanced that these two phenomena are explicable on the basis of a small amount of hybridity in the spring populations, and that the greater variance of experimental alienicolae is due in part to the survival of those anomalous and intermediate clones noted among the spring genera-

tions, which probably represent the hybrid portion of the population and which in nature do not apparently survive the spring migration.

It has been found in preliminary experiments that males of *Sappaphis crataegi* (Kltb.) from carrot will copulate spontaneously with oviparae of *S. kunzei* (Börner), the progeny of wild gynoparae collected from parsnip, when other oviparae are not present, and that apparently initially viable ova are laid.

It has been seen that spring gall samples with low grade or incomplete expression of the morphological characters of *S. petroselini* (Börner) have been collected on various occasions from bushes where they occurred together with samples of pure *petroselini* and one or more other taxa—i.e. where the prerequisite conditions for hybridization had existed during the previous autumn. Further, in at least one series of tests (T.2, 4, 8 and 9, 1952) such intermediate gall samples have been found non-responsive to the hosts of all the other short-haired taxa, so far as could be judged from failure to establish any colonies upon them in choice tests. In no case have colonies with intermediate expression of *petroselini* characters been found on secondary hosts in the field.

Occasional samples of aphids intermediate in hair length between the long- and short-haired groups have been found in the field on *Pastinaca sativa*. This is the normal summer host of *S. kunzei* (Börner) in the short-haired group, and apparently has also a limited acceptability to *S. lauberti* (Börner) (long-haired group) both in the field and in transference experiments. It might therefore be supposed that a putative hybrid *lauberti* \times *kunzei* would have less difficulty in accepting and colonizing *Pastinaca* than would be experienced by the majority of other possible hybrid combinations in trying to find a secondary host. In this connection it is interesting also to note that an occurrence of this kind was recorded in 1950 on a stretch of road verge in Cambridgeshire where it was known that some plants of *Pastinaca* had come into flower precociously in May; since the normal host of *lauberti*, *Heracleum sphondylium*, normally flowers first about a month before *Pastinaca* this may not be without significance.

These various findings, none of which by itself is conclusive, together make a picture which points very forcibly to the conclusion already discussed as a hypothesis: that the complex of *Sappaphis* using hawthorn as primary host, with the probable exception of *S. ranunculi*, are capable of viable hybridization, and that the spring generations regularly contain a certain proportion of such hybrids, whose characters in some cases are so intermediate between the parent forms as to complicate the taxonomy of the group very considerably. In general these hybrid forms do not survive, probably because, while their viability on *Crataegus* is normal, their secondary host-finding reactions are so abnormal as to lead to their elimination by the rigours of the spring migration.

The effect of such a state of affairs on the evolution of the group will not be appreciable once the various taxa have diverged to the point of having mutually exclusive secondary host relationships, since the hybrids will almost certainly not survive until the following sexual generation in the ensuing autumn. It thus appears that in actual fact isolation through secondary host preference can exist even in groups where crossability on a common primary host still exists, provided that the secondary host relations are sufficiently specific to place hybrids at a strong enough selective disadvantage to cause their virtual elimination during the spring migration. This is the converse of the argument presented in the discussion of biological characters (Section 6a); and from it we may derive the postulate that the advantages of evidence obtained from transference tests to secondary hosts vary inversely as the survival rate (including sexual fertility) of hybrids produced in nature by the species under consideration. This further leads to the comfortless conclusion that it is precisely in those cases where morphological methods of taxonomy are most likely to be stultified by a high hybrid survival rate in the population that the relative advantage of biological evidence from such transference tests is reduced to a minimum. This is under-

lined in fact by the inconclusive results of attempts to separate *Sappaphis crataegi* and *S. kunzei* during the present investigation.

The characters of the various *Sappaphis* on *Crataegus* have already been dealt with in the general discussion. The general conclusions on their taxonomy to which this investigation has led may be summarized as follows :

There are two species-groups of *Sappaphis* using *Crataegus* as primary host : one consists of the single species *S. ranunculi* (Kltb.) ; the other may best be regarded as the product of the progressive fragmentation of a single ancestral stock migrating between *Crataegus* and Umbelliferae. The evidence provided by the number of different characters by which it differs from the other members of the group points to an early separation of *S. petroselini* (Börner) from the main stock ; this was later followed by the separation of the long-haired *lauberti* (Börner) and *angelicae* (Koch) from the short-haired *crataegi* (Kltb.) ; while the last-named has recently diverged into subspecies *crataegi* s. str. and *aethusae* (Börner), and is in process of further divergence into races (and ultimately species) associated with *Daucus carota* and *Pastinaca sativa* respectively. The *Pastinaca* race has already been named as a species (*kunzei*) by Börner ; in this he must be held to have anticipated the end-product of evolution.

Viable hybrids can probably be produced between any members of the second species-group ; but it is probably only in the case of the incipient divergence of *crataegi* and *kunzei* that such hybridization has any effect in breaking down isolation and retarding the divergence of the species composing the complex.

These conclusions still require much confirmatory work before they can be regarded as finally proved. For this work various techniques might be considered, such as chromosome studies, comparative serology, paper partition chromatography and more extensive crossing experiments. It is thought that the last two methods offer the best hope of getting the desired results in a conclusive form, and it is hoped to follow up with some further work on these lines at a later date. Meanwhile, this account is to be regarded as an interim discussion of the problem, which it is hoped may stimulate other workers to apply this kind of programme to other critical groups, such as the black *Aphis* complex, where similar conditions may be found.

13. SUMMARY.

The taxonomy of the British species of *Sappaphis* Matsumura using *Crataegus* as primary host has been investigated by means of free choice transference tests to secondary hosts and biometric studies on both wild material and experimental cultures derived from transference tests.

The results confirm the existence of seven different taxa causing galls on *Crataegus* leaves in spring. These belong to two species-groups, one consisting only of *S. ranunculi* (Kltb.) and the other of four species (*S. lauberti* (Börner), *angelicae* (Koch), *petroselini* (Börner) and *crataegi* (Kltb.)), one subspecies (*S. crataegi* ssp. *aethusae* (Börner)) and one biological race or infrasubspecies of *S. crataegi* (*kunzei* Börner). The existence of other subspecies of *S. crataegi* proposed by Börner (*anthrisci* and *aegopodii*) has not been confirmed in extensive field collections, and as no morphological diagnoses have been given these are regarded as *subspecies dubiae* in view of the not infrequent records of anomalous host choice in this group of *Sappaphis*. All members of the group have been found to be about equally abundant in the Cambridge area, with the exception of *angelicae* whose distribution is limited by its secondary host *Angelicae sylvestris* ; but relative abundance of the different species fluctuates from year to year.

Examination of data for nymph colour in galls on *Crataegus* and degree of wax powdering is held to discredit the use of these characters for taxonomic purposes in *Sappaphis*. Examination of hair lengths show that these can vary within limits which do not invalidate them as taxonomic characters except in *S. ranunculi* (Kltb.) ;

an estimate of limits of variability for abdominal hair length maxima within the second (*crataegi*) species-group points to a limiting value of about 24 for the Coefficient of Variability within homogeneous samples.

It appears that certain phenomena arising in the analysis of variance data for certain characters in wild and experimental material, together with observations on the characteristics of field collections from *Crataegus* and secondary hosts, can most simply be accounted for by the existence of a proportion of hybridity among the population on *Crataegus* in spring. A preliminary experiment shows that cross-mating is possible between *Sappaphis crataegi* (Kltb.) and its biological race *kunzei* Börner.

Although transference tests from *Crataegus* to secondary hosts were used as a valuable complement to morphological studies it has been deduced from theoretical considerations that such tests have no more intrinsic reliability than traditional morphological methods except where secondary host differences bring about effective isolation through the selective disadvantage attaching to hybrids; and they are thus no more effective than morphological methods for the detection of incipient divergences in an evolving complex.

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APPENDIX

*Data on Abnormal Host Relationships Recorded in Field Collections and Experimental Transferences.*1. *Field Collections.*

(a) *Sappaphis lauberti* (Börner).—Has been taken on *Conium maculatum* (sample 720, 25.vi.50), *Pastinaca sativa* (samples 744, 7.vii.50, and 757, 4.viii.50; also one spring migrant among sample 1336, 4.vi.54), *Smyrnum olusatrum* and *Foeniculum vulgare* (samples 56/13 and 56/11 respectively, 26/7.vi.56). The localities from which these collections were made were :

720 : North Berwick, East Lothian.

744 and 757 : Fulbourn, Cambridgeshire.

1336 : Gogmagog Hills, Cambridgeshire.

56/11 and 56/13 : Clifton Suspension Bridge, Bristol.

Samples 744 and 757 are considered to be of possible hybrid origin.

(b) *Sappaphis petroselini* (Börner).—Has been taken on *Smyrnum olusatrum* (Samples 749, 13.vii.50, and 56/6, 26.vi.56) and *Foeniculum vulgare* (sample 56/21, 27.vi.56). Localities for these samples were :

749 : Woodchurch, Thanet, Kent.

56/6 : and 56/21 : Clifton Suspension Bridge, Bristol.

(c) *Sappaphis crataegi* (Kltb.), *sensu latiori*.—Has been taken on *Smyrnum olusatrum* (samples 727, 20.vi.50, and 56/13, 27.vi.56), *Foeniculum vulgare* (sample 56/11, 26.vi.56, and 56/21, 27.vi.56) and *Myrrhis odorata* (V. F. Eastop leg., Reading Berks., 13.vi.50). Localities as previously recorded, with the addition of :

727 : Cherryhinton, Cambridgeshire.

The samples recorded above from the Clifton Suspension Bridge, Bristol, were collected from a steep and sunny slope on the Gloucestershire bank of the Avon, towards the crest of Clifton Down. Plants of *Smyrnum* and *Foeniculum* were numerous, and most had some *Sappaphis* basally. Ants were very numerous in the dry limestone soil. When the various samples collected were examined the *Sappaphis* species were found to be similarly distributed on both hosts, *S. crataegi* (*s.l.*) being the commonest with a small admixture of *S. lauberti* and *S. petroselini*. The last-named was subsequently transferred to *Petroselinum* in the insectary and produced a strong culture. This constituted the most remarkable exhibition of the "reserve host" phenomenon yet encountered.

2. *Experimental Transferences.*

The conditions under which transferences were carried out placed a premium on abnormal choices by the alatae used. Therefore the mere recovery of alatae from abnormal hosts is not regarded as in any way significant. The following records refer only to cases in which aphids and their progeny persisted on an abnormal host through one or more complete generations.

1951.

Gall series A. A sparse culture of *Sappaphis* maintained itself on a plant of *Rumex obtusifolius* from the date of transfer (28/30.v.51) up till at least 12.vii.51 (date of last sampling). Samples were taken in June (F.1), on 5.vii.51 and 12.vii.51; the two latter samples consisted of four specimens only. The plant was also very heavily infested by *Myzus ascalonicus* Donc., among which the *Sappaphis* lived dispersed, not basally concentrated like *S. radicola* (Mordv.). The morphological characters of the aphids showed that they were *S. lauberti* (Börner). This is the only

instance recorded of a member of this group of *Sappaphis* living on a secondary host other than a member of the Umbelliferae.

Gall series E. Colonization of *Smyrniolum olusatrum* was recorded by aphids which later refused to transfer from *Smyrniolum* to *Heracleum* or *Petroselinum*. They would however transfer to *Aethusa* and to a slight extent to *Daucus*. The aphids were short-haired, and agreed with the characters of *S. crataegi* (Kltb.), s. lat. It appeared that the subspecies *aethusae* Börner was responsible for colonizing *Smyrniolum*, but there may have been some admixture of *S. crataegi* s. str. This result is comparable with field data and with the records for gall series F and M.

Gall series F. In both replicates of the tests carried out with this series the only hosts accepted were *Heracleum*, *Aethusa* and *Smyrniolum*. The aphids living on *Smyrniolum* were found in each case to be a mixture of long- and short-haired aphids corresponding with the characters of *lauberti* and *crataegi* ssp. *aethusae*. This is interesting as confirming the possibility of coexistence of two different taxa intermingled on a reserve host, recorded in the field at Bristol (see paragraph 1), and due in part probably to the lack of selective advantage of one species over the other on a plant which is not naturally a host of either.

Gall series M. *Smyrniolum olusatrum* was colonized by aphids with the characters of *S. crataegi* s. lat.

Gall series I. *Pastinaca sativa* was colonized by aphids whose progeny had the morphological characters of *S. lauberti*. Samples were taken on 18.vi.51 and 5.vii.51. No other aphids occurred with them, and colonization was rather dispersed and on the leaves rather than at the bases of the petioles.

1952.

Gall series P and Q. Gall samples with green nymphs from these two series colonized only *Apium* and *Petroselinum* successfully; but on 13.vi.52 two adult apterae agreeing with *petroselini* were recovered from *Pastinaca sativa*, on which they had apparently survived with difficulty.

Gall series T. Colonies were formed on *Petroselinum* and *Aethusa*. The former calls for no remark, being pure *petroselini*; the latter colony, which was on a plant heavily contaminated with *Myzus ascalonicus* Donc., was sampled on 31.v.52 and 13.vi.52, when the sample constituents were found to be a mixture of *S. crataegi* ssp. *aethusae* and *S. petroselini*. By the second sampling date the *petroselini* were predominant.

1953.

Gall AA. *Daucus carota* was successfully colonized; *Pastinaca* and *Petroselinum* were rejected. A weak colonization took place on *Aethusa* and *Torilis*; 9 F.1 apterae were ultimately reared on the former and three small ones on the latter host. In both cases the F.1 took much longer to reach maturity than the F.1 of the *Daucus* colony. This was the only recorded instance of *crataegi* s. str. being able to colonize the hosts of ssp. *aethusae*; the converse colonization has not yet been recorded, although recognition of such a situation in the field would be very hard owing to the very small morphological differences between the subspecies.

A NEW SPECIES OF PTYCHOTREMA MÖRCH (MOLLUSCA: GASTROPODA) FROM TANGANYIKA TOGETHER WITH A CHECK LIST OF THE EAST AFRICAN SPECIES AND KEYS FOR THEIR DETERMINATION.

By B. VERDCOURT.

(With 2 Text-figures.)

[Read 21 November 1957.]

A West African type fauna and flora extends into Uganda, parts of W. Kenya (Nyanza) and parts of the Lake and Western Provinces of Tanganyika. Elsewhere in East Africa this type is rarer but elements occur in the montane forests. The genus *Ptychotrema* is a good example. It is represented by a few species in Kenya and Tanganyika but becomes more abundant in Uganda particularly in the Ruwenzories. There are however certain distinctive W. African elements in the rain forest fauna and flora of the East Usambara mountains, which are situated only about 40 miles from the east coast of Africa. A complete but popular illustrated account of the Gulellae of these mountains is being published in *Tanganyika Notes and Records* shortly. During the preparation of that account a new species of *Ptychotrema* was discovered in both the East and West Usambaras. It is the first member of that genus to be reported from the area. Some striking W. African plants such as *Gardenia abbeokuta* Hiern also occur there.

The genus *Ptychotrema* belongs to the family Streptaxidae which is a dominant element in the molluscan fauna of tropical Africa. All the members are carnivorous and have radulae with large aculeate teeth. *Ptychotrema* is closely related to *Gulella* Pfr. but differs in having one to two spiral furrows externally on the body whorl. The species live under debris on forest floors, particularly in rain forests. The feeding habits of the larger streptaxids are well known and they are frequently to be observed feeding on Achatinidae and Urocyelidae but the smaller species may also live on decaying matter. In certain habitats the total number of individuals of minute streptaxids exceeds the number of snails belonging to other families which suggests that they are not entirely carnivorous since food supplies would rapidly be exhausted.

In December 1949 the writer discovered a single shell (Verdcourt P) at Mkusi near Lushoto in the West Usambaras. This was sent to Dr. K. L. Pfeiffer for identification but he died before studying it. The shell is now in the Senckenberg Museum, Frankfurt. During nearly a year's stay in Amani, E. Usambaras in 1950 I found no further examples, but in April 1954 a juvenile was found. In December 1956 three examples were found at Amani by my wife and myself, thus enabling the species to be described.

***Ptychotrema (Parennea) usambarensis* Verdcourt sp. nov.**

Testa cylindrica, apice obtusa, albida vel dilute flavida, striis brunneis irregulariter notata. Anfractus 8·5 to 9, vix convexiusculi, superiores tres laeves, caeteri costati, ultimo basi attenuato circa rimam compresso, sulco profundo suturae parallelo constricto. Apertura semiovalis, dentibus 2 munita, altero lamelliformi juxta insertionem, altero conico in medio marginibus dextri. Peristoma crassum, nitidulum, minute rugulosum, expansum, marginibus callo crasso junctis. Longit. 5·5 mm., diam. 2·5 mm.

Shell cylindrical, broadest at the middle, apex rounded, colourless or faintly tinged yellowish, spire with very irregularly scattered vertical brown streaks which occupy spaces between the ribs and give a highly characteristic appearance to the shell. In side view the shell is distinctly clavate and considerably narrowed at the base. Whorls about 8·5 to 9, slightly convex, the last with a shallow but conspicuous furrow encircling its middle. Apical three whorls relatively smooth compared with

the rest which are very strongly ribbed. First whorl almost smooth, next two with faint broad vertical striae and rather obscure spiral elements; these three apical whorls have a marked furrow just below the suture which is bordered by a sharp edge but this becomes barely perceptible on the later whorls. The later whorls are very strongly ribbed with slightly curved costae (6 to 7 per mm.) which are about as wide as the interstices which show faint traces of a spiral element in some cases. Aperture semi-oval, the peristome continuous and thick save in the corner to the right of the parietal lamella where there is a conspicuous gap; the peristome is not entirely smooth but the surface of the callus is finely shagreened. Parietal lamella strong but short, slightly curved, margin of peristome ascending to the right of it. There is a single strong denticle about half-way up the labrum which is the lower boundary of a sinus bounded on the other side by the parietal lamella. These two teeth extend inwards for some distance and their margins are parallel, the gap between the two being about 0.3 mm. The labral lamella extends back into the interior and then becomes obscure but after a distance equivalent to 7 ribs becomes clearly evident again and encircles the shell for over a whorl and corresponds to the external furrow. The columella and parietal areas of the peristome are thick and shining and devoid of denticles. There is a faint furrow between the two areas. A very slight fold is noticeable inside the shell at this corner of the aperture. Height of shell: 5.5 mm., breadth of shell 2.5 mm. Height of aperture 1.6 mm., breadth of aperture 1.8 mm. All four specimens have almost identical dimensions. Animal unknown. (Figs. 1 and 2).

TANGANYIKA: East Usambaras, Amani, Mt. Bomole, amongst moss and sticks under *Cupressus* plantation in rain forest area, 900 m. alt., April 1954, one juvenile, *B. Verdcourt* (Coryndon Museum collection); same locality, December 1956, *B. Verdcourt* (holotype in Coryndon Museum, paratype in British Museum (Natural History), paratype in Congo Museum, Tervuren). West Usambaras, Mkusi, near Lushoto, in dry evergreen forest, December 1949, *B. Verdcourt* (in collection of Senckenberg Museum ex collection K. L. Pfeiffer).



FIG. 1.

FIG. 1.—Holotype of *Ptychotrema usambarense* Verdcourt.

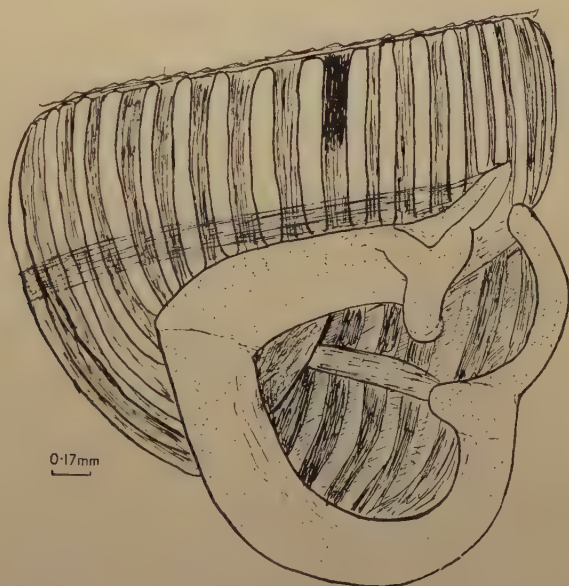


FIG. 2.

FIG. 2.—Aperture of latter, enlarged.

This new species may be separated from the other species of the subgenus *Parennea* by the following key.

- 1 Shell smooth or with only the sutures crenellate and slight growth lines; area immediately behind peristome may be striate or with a few thick ribs 2
Shell striate to strongly ribbed 5
- 2 Aperture possessing a small second labral tooth and a small basal denticle apart from the main parietal and labral teeth (E. Kenya) **sperabile** (Prest.)
Aperture with only the two main teeth 3
- 3 Shell narrowly cylindrical, 4.35×1.6 mm. with 7.5 whorls, nearly smooth (Congo) **cylindrus** Pilsbry
Shell cylindrical or oblong-cylindric, $2.5-3.5$ mm. long, sutures crenulate 4
- 4 Shell cylindrical, $3.2-3.5$ mm. long and $1.45-1.5$ mm. broad (race *tshibindanum* Pilsbry & Cockerell differs only slightly) (Congo) **nyangweense** Pilsbry
Shell oblong-cylindrical, 2.55 mm. long and 1.25 mm. broad (Congo)
- 5 Labral fold not reaching the peristome to form a tooth; shell 2.8×1.5 mm. (W. Kenya) **mukulense** Pilsbry
Labral fold forming a strong tooth at the peristome **cedrorum** Connolly
- 6 Shell larger, $7-7.5$ mm. long 6
Shell under 6 mm. long 7
Shell 7×4 mm., suture not crenulate; labral tooth conic (Angola) 8
- 7 Shell 7.5×3.75 mm., suture crenulate; labral tooth slightly bifid (Congo) **circumcisum** (Morelet)
Shell 7.5×3.75 mm., suture crenulate; labral tooth slightly bifid (Congo) **connollyi** Dupuis & Putzeys (= *dykeiana* Spence)
- 8 Shell cylindrical, strongly ribbed, apex obtuse, upper whorls with furrow below the suture, 5.5×2.5 mm. (Usambaras) **usambarenses** Verdcourt
Shell ovate or much smaller 9
- 9 Shell oblong-cylindric, faintly striate, columella conspicuously binodulate, 2.25×1.1 mm. (Congo) **scintilla** Pilsbry & Cockerell
Shell ovate or ovate-oblong, larger, at least 3.2 mm. long; striae more obvious 10
- 10 Shell with 7 whorls, 4.25×2.25 mm., ovate, coarsely striate (Mt. Kenya) **syngenes** (Prest.)
Shell with 6 whorls, 3.25×1.75 mm., ovate, less coarsely striate (Mt. Kenya) **uniliratum** (Smith)
Shell with 5.5 whorls, 3.6×2 mm., ovate, acute, strongly ribbed (Congo and Uganda) **aequatoriale** Pilsbry
Shell with 6.5 whorls, 4.54×2.25 mm., ovate-oblong or \pm cylindrical, fairly strongly ribbed (Angola and Uganda) **sulciferum** (Morelet)

Note.—I have not seen the type of *P. sulciferum* but only two Uganda specimens named by Connolly and one found in the stomach of the bird *Cossypha cyanocampter* (Bonaparte) by Mr. J. G. Williams in the Bwamba Forest, Uganda.

LIST OF THE SPECIES OF *Ptychotrema* KNOWN FROM EAST AFRICA.

Note.—A careful perusal of all the Gulellae recorded from East Africa might add to the number of species of *Ptychotrema*, particularly if the section *Wilmattina* is retained in this genus. The descriptions are often not adequate to decide the genus.

Ptychotrema Mörch, 1852.

Subgenus *Ptychotrema*.

Section *Haplonepion* Pilsbry, 1919.

P. supradentatum (Thiele, 1911).

TANGANYIKA, LAKE RUKWA area.

Ennea supradentata Thiele, *Wiss. Ergebn. D.Z. Afr. Exp.* (1907-8), 3, 177, pl. 4, f. 5-6 (1911).

P. geminatum (von Marts., 1895).

UGANDA, RUWENZORI.

Pilsbry, *Bull. Am. Mus. Nat. Hist.*, 40, 201, text-f. 70 (1919).

Ennea geminata von Marts., *Nachrichtsbl. D. Malak. Ges.*, 27, 177, (1895) and in *Deutsch Ost-Afr.*, 4, Beschalt. Weichth., 27, pl. 2, f. 26 (1897); Thiele, *loc. cit.*, 177, pl. 4, f. 8,

P. runsoranum (von Marts., 1892).

UGANDA, RUWENZORI.

Pilsbry, *loc. cit.*, 202.*Ennea runsorana* von Marts., *S.-B. Ges. naturf. Fr.*, **1892**, 179 (1892).*E. runsorana* von Marts., *Beschalte Weichth.*, 28, pl. 2, f. 25 (1897); Thiele, *loc. cit.*, 178, pl. 4, f. 9.**P. edgarianum** Pilsbry, 1919.

UGANDA, RUWENZORI.

Pilsbry, *loc. cit.*, 204, text-f. 73.**P. limbatum** (von Marts., 1892).

UGANDA, RUWENZORI.

Pilsbry, *loc. cit.*, 205, text-f. 74.*Ennea limbata* von Marts., *S.-B. Ges. naturf. Fr.*, **1892**, 178 (1892) and in *Beschalte Weichth.*, 26, pl. 2, f. 23 (1897).*Ptychotrema fisheri* Connolly, *Ann. Mag. Nat. Hist.* (9), **10**, 489, pl. 14, f. 32 (1922); later put into synonymy by author, *Proc. Malac. Soc.*, **19**, 38 (1930).**P. kombaense** (Prest., 1913).

UGANDA, KOMBA.

Ennea kombaensis Prest., *Proc. Zool. Soc. Lond.*, **1913**, 216, pl. 34, f. 4 (1913).**P. ujijiense** (Smith, 1880).*Ennea ujijiensis* Smith, *Proc. Zool. Soc. Lond.*, **1880**, 347, pl. 31, f. 5 (1880).**P. quadrinodatum** (von Marts.) most probably occurs on the UGANDA side of the RUWENZORIES.Pilsbry, *loc. cit.*, 201.*Ennea quadrinodata* von Marts., *Nachrichtsbl. D. Malak. Ges.*, **27**, 177 (1895) and in *Beschalte Weichth.*, 27, pl. 2, f. 24 (1897); Thiele, *loc. cit.*, 177, pl. 4, f. 7.Subgenus *Ennea* H. & A. Adams, 1855.**P. masakaense** (Prest., 1913).

UGANDA, MASAKA.

Ennea masakaensis Prest., *Proc. Zool. Soc. Lond.*, **1913**, 209, pl. 34, f. 9 (1913).**P. superadornatum** Germain, 1934.

KENYA, ELGON.

Germain, *Bull. Mus. Hist. Nat.*, Paris, **1934**, 263 (1934) and figured after author's death by editors of *J. Conchyl.*, **92**, 162, pl. 7, f. 2, (1952).**P. bequaerti** (Dautz. & Germain, 1914).

UGANDA, IBANDA, ENTEBBE.

Pilsbry, *loc. cit.*, 207; Venmans, *Basteria*, **18**, 40-44, text-figs. 1-4 (1954).*Ennea bequaerti* Dautz. & Germain, *Rev. Zool. Afr.*, **4**, 5, pl. 3, f. 14 (1914).**P. polloneræ** (Prest.) and **P. paradoxulum** (von Marts.) will probably be found on the UGANDA side of the RUWENZORIES. They are figured by their authors as follows :*Ennea polloneræ* Prest., *Proc. Zool. Soc. Lond.*, **1913**, 213, pl. 35, f. 9 (1913).*Ennea paradoxula* von Marts., *S.-B. Ges. naturf. Fr.*, **1895**, 122 (1895) and *Beschalte Weichth.*, 29, pl. 2, f. 34 (1897).Subgenus *Parennea* Pilsbry, 1919.**P. uniliratum** (Smith, 1903).

KENYA, MT. KENYA and MAU.

Ennea unilirata Smith, *J. Conch.*, **10**, 315, pl. 4, f. 8 (1903).**P. syngenes** (Prest., 1913).

KENYA, MT. KENYA.

Ennea syngenes Prest., *Proc. Zool. Soc. Lond.*, **1913**, 216 (1913).*E. consobrina* Prest., *Ann. Mag. Nat. Hist.* (8), **7**, 463, pl. 11, f. 1 (1911) non Ancey.

P. sulciferum (Morelet, 1883). UGANDA, BWAMBA and ENTEBBE.
Ennea sulcifera Morelet, *J. Conchyl.*, **31**, 410, pl. 10, f. 6 (1883).

P. aequatoriale Pilsbry, 1919. UGANDA, ENTEBBE.
 Pilsbry, *loc. cit.*, 213, text-f. 83.

P. cedrorum Connolly, 1922. KENYA, UASIN GISHU and TURI.
 Connolly, *Ann. Mag. Nat. Hist.* (9), **10**, 490, pl. 14, f. 13 (1922).

P. usambarense Verdcourt, 1958. TANGANYIKA, USAMBARAS.

P. sperabile (Prest., 1910). KENYA, SHIMBA HILLS.
 (See below for further discussion of this species)

Uncertain.

P. stuhlmanni (von Marts., 1892). UGANDA, BUDDU COAST.
Ennea stuhlmanni von Marts., *S.-B. Ges. naturf. Fr.*, **1892**, 16 (1892) and in *Beschalte Weichth.*, 28, pl. 2, f. 27 (1897).

(Note.—This may be a *Parentnea*. It is distinguishable from any other East African species in either *Ennea* or *Parentnea* by its second parietal tooth coupled with its small size (4×2 mm.) and strong striae.)

Subgenus *Wilmattina* Pilsbry & Cockerell, 1933.

This subgenus was erected for species formerly included in *Gulella* which have a deeply immersed palatal ridge. Pilsbry placed in this the shell he had named in 1919 as *G. disseminata cymatonotus*. In his later paper he explains that this subspecies has a deeply hidden palatal ridge and should be referred to *Wilmattina* and raises the subspecies to specific rank. He does not mention if typical *disseminata* should be referred to the new subgenus, nor why he considers the subspecies specifically distinct. I have examined some *G. disseminata* (not the types recently however) and find there are traces of a deeply inset palatal fold. I am not sure, however, if this group is not really more akin to the true *Gulellae*. Of the East African forms the subgenus would include the following:

P. disseminatum (Prest., 1913). UGANDA, KENYA.
Ennea disseminata Prest., *Proc. Zool. Soc. Lond.*, **1913**, 202, pl. 33, f. 2 (1913).

E. ingeziensis Prest., *loc. cit.*, 204, pl. 33, f. 9 (1913).

E. burungaensis Prest., *loc. cit.*, 206, pl. 32, f. 12 (1913).

Gulella disseminata (Prest.), Connolly, *Ann. Mag. Nat. Hist.* (9) **10**, 496 (1922).

P. disseminatum kekumegaense (Connolly, 1922). KENYA, KAKAMEGA
Gulella disseminata kekumegaensis Connolly, *Ann. Mag. Nat. Hist.* (9), **10**, 496, pl. 14, f. 14 (1922).

Note on *Ennea sperabile* Preston.

Ptychotrema (Parentnea) sperabile (Prest.).

Ennea sperabile Prest., in *Ann. Mag. Nat. Hist.* (8), **6**, 528, pl. 7, f. 6 (1910).

During a rapid survey of the Streptaxidae in the British Museum, I made a note of the fact that I considered *Ennea sperabile* Prest., to be a *Ptychotrema* and close to the shell I remembered collecting in the West Usambaras several years before. I am indebted to M. Benoit of the Congo Museum, Tervuren for loaning me the holotype of this species for a more careful study. It is similar to *P. usambarense* in size and in

the non-continuity of the peristome in the top right-hand corner and also in the shape of the aperture. It differs in very many other respects. The shell is smooth save for ribs just behind the aperture. There is a minute inset basal tooth which is mentioned by Preston but there is also a small inset labral tooth just below the main labral tooth which he does not mention. I have refigured the species (Fig. 3).



FIG. 3.—Holotype of *Ptychotrema sperabile* (Prest.).

KEYS TO THE REST OF THE EAST AFRICAN SPECIES OF *Ptychotrema*.

To render this paper more useful, keys are given to the subgenera *Ennea* and *Ptychotrema*. These have partly been compiled from the literature and partly from specimens.

KEY TO EAST AFRICAN SPECIES IN SECTION *Haplonepion*.

- | | | | |
|---|---|-------------|----------------------|
| 1 | Shell large, over 10 mm. tall (usually over 12 mm.) | — | 4 |
| | Shell smaller, usually under 9 mm. tall | | 2 |
| 2 | Columella with only a very obscure bifid fold, shell 7×3.2 mm. | | kombaense |
| | Columella with at least 3 prominent internal folds | | 3 |
| 3 | Shell elongate, 8–9 mm. long | | runsoranium |
| | Shell small, ovate, 3.5–4.7 mm. long | | edgarianum |
| 4 | Columella with more obscure internal folds, suture crenellate (W. Tanganyika) | | 5 |
| | Columella with pronounced folds, if suture crenellate then columella with external marginal denticles as well | | 6 |
| 5 | Columella with 2 small folds, lip folds not reaching margin, 2 main ones and 1–2 minor ones; shell probably 19×5.3 mm. | | ujijiense |
| | Columella with 3 small folds, lip with small denticle and 3 inner folds below | | supradentatum |
| 6 | Columella with 2–3 external marginal denticles as well as 3 internal folds, shell $14\text{--}16 \times 6$ mm. | | limbatum |
| | Columella with internal folds only | | 7 |
| 7 | Three folds on outer lip, shell $11\text{--}14 \times 4.4\text{--}5$ mm. | | geminatum |
| | Four folds on outer lip, shell $16\text{--}19 \times 6$ mm. | | quadrinodatum |

KEY TO THE EAST AFRICAN SPECIES IN THE SUBGENUS *Ennea* (INCLUDING TWO SPECIES WHICH MAY OCCUR).

- 1 Shell large, 12×6.75 mm.; a bifid fold at the top of the columella and 2 ridges inside outer lip, the upper of which ends in a denticle **pollonerae** 2
Shell much smaller 2
- 2 Outer lip folds either not reaching the margin or ending only in a faint angulation 3
Upper outer lip fold ending at margin in a denticle 4
- 3 Shell $2.5-2.8 \times 1.4-1.6$ mm., ovate; columella with no folds **superadornatum**
Shell 6.1×2.5 mm., oblong; columella with 3 weak nodules **bequaerti**
- 4 Columella with no folds, shell 4×1.75 mm. **masakaense**
Columella with 2 folds, shell 4.5×1.5 mm. **paradoxulum**

SUMMARY.

A new species of *Ptychotrema* is described from N.E. Tanganyika and the correct position of *Ennea sperabile* Prest. demonstrated. A list and keys are given for the rest of the E. African species.



4

